1991

Ecology of Heracleum lanatum Michx. (cow parsnip) communities in northwestern Montana

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ECOLOGY OF HERACLEUM LANATUM MICHX. (COW PARSNIP)

COMMUNITIES IN NORTHWESTERN MONTANA

By

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Presented in partial fullfillment of the requirements for the degree of

Master of Science

UNIVERSITY OF MONTANA

1991

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June 12, 1991
Date

UMI Number: EP38198

Campbell, Robert B., Jr., M.S., June 1991 Forestry

Ecology of Heracleum lanatum Michx. (Cow Parsnip) Communities in Northwestern Montana (118 pp.)

Director: E. Earl Willard E.E.W.

Heracleum lanatum, a tall, hollow-stalked, long-lived perennial in the Apiaceae (parsley family) is considered important for a number of desirable traits: early spring green-up; abundant amounts of lush biomass; and high palatability for cattle, sheep and certain wildlife species. The presence of this species has been linked to key grizzly bear habitats. An extensive literature review reports the life history attributes and historical values and uses of H. lanatum.

This study's first objective was to identify the probable key environmental factors which influence the occurrence and abundance of H. lanatum. Percent cover of all plant species on all plots was analyzed by Detrended Correspondence Analysis (DCA) and Two-way Indicator Species Analysis (TWINSPAN) and correlated with environmental variables. Based on the 49 stands of H. lanatum sampled, this species grows most abundantly in microsites that are depositionally disturbed, receive water in excess of annual precipitation and have undulating floodplains with slopes less than 5% adjacent to streams. This species does not grow well under conifer canopies. Neither aspect, elevation, soil texture, percent organic matter, nor size of stand correlated with the abundance of H. lanatum.

The second objective of this study was to identify plants commonly associated with H. lanatum. Based on the DCA and TWINSPAN analyses, seven species were closely associated with this species: Alnus incana, Calamagrostis canadensis, Carex bebbii, Elymus glauca, Geum macrophyllum, Rubus idaeus and Urtica dioica.

Management recommendations include the following suggestions: protect sites where H. lanatum is established and growing abundantly; introduce this species to a site either by seed or transplants; select target sites with the environmental attributes of ideal sites and some of the closely associated species present; sow H. lanatum seed in the fall to stratify seed and meet cold treatment requirements for germination naturally; and expect extremely slow development for new seedlings.

ACKNOWLEDGEMENTS

I express my appreciation to my committee members, Dr. James R. Habeck and Dr. Robert D. Pfister, for their guidance and encouragement from the planning stages to the final product and their patience in waiting for the results. I am greatly indebted to Dr. E. Earl Willard for his direction as committee chair. His suggestions and advice provided substantial improvements at all stages of the study. As the completion of this study neared, I relied heavily on his support and tireless assistance.

This study was funded entirely by the USDA Forest Service's Wildlife Habitats Research Work Unit from the unit's operating budget under study number 4201(2). Special appreciation goes to Dr. L. Jack Lyon, project leader of the Wildlife Habitats Unit, Intermountain Research Station, Forestry Sciences Lab, Missoula, Montana, for allowing me to study cow parsnip while a permanent employee of the same unit.

Cover for all plant species on the plots was the major variable underlying this study. Thanks go to Peter F. Stickney, plant ecologist with the Wildlife Habitats Unit, for his expertise with identification and verification of the over 400 voucher specimens collected during the field work. Beyond that, I cherish his support as a friend; his enthusiastic dedication to the study of plants is an inspiration to me.

Dr. Cliff J. Martinka, senior scientist for Glacier National Park, encouraged me to do a gradient analysis for cow parsnip and coordinated my data collection for the study sites in the park. I appreciate the hospitality and cooperation of his research staff at Glacier National Park.

Because of the difficulties in texturing soils high in organic matter, I valued greatly the able experience of Arial "Andy" Anderson, retired soil specialist formerly with the Soil Conservation Service, who determined the textures for the horizons in all of the soil profiles.

And last, but certainly not least, I express my appreciation to my wife, Glynis, and our sons, Ross, Ryan, Steve and Paul, for their support and patience through all the years that I worked on this study.

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OBJECTIVES

Introduction

Heracleum lanatum Michx. (cow parsnip), a tall, hollow-stalked, long-lived perennial in the parsley family, is native to an extensive portion of North America. Its distribution extends from California to Alaska and eastward to Newfoundland and Georgia. *H. lanatum* typically grows in moist riparian sites and also frequents avalanche chutes, seep areas on upland slopes and even some wet roadsides. It occurs from sea level to above 10,000 ft. This species is considered important for a number of desirable traits including the following: early spring green-up; abundant amounts of lush biomass; and high palatability for cattle, sheep and certain wildlife species. Yet, the literature of *H. lanatum* has many broad gaps about its ecological life history.

Numerous studies have linked the presence of *H. lanatum* to key grizzly bear habitats. At the Grizzly Bear Habitat Symposium (Contreras and Evans 1986), 11 of the 33 papers mentioned *H. lanatum*. Jonkel and Hadden (1986) prioritized 10 grizzly bear habitat research needs. A better understanding of *H. lanatum* communities will apply directly to their top four research priorities. Kendall (1986) showed that *H. lanatum* comprised 15% of the biomass (the greatest amount from a single species) consumed annually by grizzlies and black bears in Glacier National Park. Wildlife biologists on the Kootenai National Forest attempted to establish *H. lanatum* in some recent clearcuts by direct seeding (Garcia 1986), but their attempts were unsuccessful. The following study was in direct response to needs expressed by wildlife biologists.

Problem Statement

The purpose of this study was to identify and describe plant communities in northwestern Montana where *H. lanatum* grows, with emphasis on those communities where it is abundant. The study had two objectives:

1. Identify the probable key environmental factors which influence the occurrence and abundance of *H. lanatum*.
2. Identify plants (ecological equivalents) commonly associated with *H. lanatum* which might serve as indicators of suitable areas for the introduction or an increase in the abundance of *H. lanatum*.

LITERATURE REVIEW

An excerpt from Pelton (1951) prefaces this literature review and this study. "...the solving of most of the ecological problems concerning even a single species would require much more time and effort than is ordinarily available to one person. Consequently most autecological data accumulate over extended periods of time from numerous studies which are of a local or limited nature and of short duration, rather than from the more desirable detailed and comprehensive long term studies. There is a need, however, for survey studies which integrate the known ecological data concerning a given species, clarify the important problems, and attempt to fill in some of the wider gaps in our knowledge of the species." In the spirit of Pelton, my intent for the study of Heracleum lanatum was: 1) to pull together the ecological facts about the species that were already published and 2) to fill in some of the gaps with my own research.

The review revealed an abundance of interesting but scattered details. However, there is not a single comprehensive source of information about this species. The literature is not exhaustive, yet several discrepancies exist even, in the more current literature, about some of the basic characteristics of this species. Many floras give general descriptions that do not always agree. I cite those which appear to have the most accurate description of this species.

Nomenclature

Hitchcock et al. (1971) only list one species in the genus Heracleum. However, differences of opinion and controversy surround the scientific name. Following an extensive literature review I have decided to use Heracleum lanatum Michx. (Bailey 1935, Abrams 1951, Booth and Wright 1966, Hitchcock et al. 1971, Hitchcock and Cronquist 1973, Redente et al. 1982, Vance et al. 1984) as the accepted Latin name. However, other Latin names are, or have been, attributed to this species: H. douglasii (Brummitt 1971, Hitchcock et al. 1971), H. maximum (Fernald 1950, Brummitt 1971), H. montanum (Brummitt 1971), H. sphondylium (Van Bruggen 1976, Dorn 1984), H. sphondylium ssp. lanatum (Love 1982), H. sphondylium var. lanatum (Dorn 1988), H. sphondylium subsp. montanum (Brummitt 1971, Weber 1976, McGregor and Barkley 1977, Weber 1987), H. sphondyllium, Pastinaca lanata (Hitchcock et al. 1971) and Sphondylium lanatum (Hitchcock et al. 1971). Common names for this species include cow parsnip (Hitchcock et al. 1971, Van Bruggen 1976, Weber 1976, Dorn 1984, 1988; Weber 1987), common cowparsnip (Plummer et al. 1955, 1968; Redente et al. 1982), cowparsnip, cow-parsnip (Bailey 1935, Fernald 1950, Abrams 1951, Booth and Wright 1966, Hitchcock and Cronquist 1973, Vance et al. 1984), cow cabbage, cow-cabbage, eltrot (Fernald 1950, McGregor and Barkley 1977), heltrot (Fernald 1950), hog weed, hogweed, hog-weed (Fernald 1950), masterwort (Fernald 1950), pie plant, pieplant and wild-pieplant. Many of these common names are used in the European literature for the species H. sphondylium (including varieties and subspecies), and this name is used in many of the floras for states or regions in the United States, particularly in the West.

Hitchcock et al. (1971) is an accepted authority for the flora of western Montana. I valued the information the authors provided and elected to follow their nomenclature. However, before I finalized my decision to use _H. lanatum_, I wrote to two authorities on the family Apiaceae/Umbelliferae. Dr. Lincoln Constance indicated that the proper name is largely a matter of personal choice but suggested that I would be well advised to use _H. lanatum_ (personal communication dated April 8, 1985). Also, I inquired of Dr. Arthur Cronquist in view of his preparation of the manuscript for the _Intermountain Flora_. He explained his rationale for using _H. lanatum_ in the draft with respect to the confusing synonymy that surrounds this taxon (personal communication dated April 11, 1985).

Life History Overview

Description of the Species

Hitchcock et al. (1971) describe the plant as a robust, single-stemmed, perennial with a stout tap root or a cluster of fibrous roots. Wooly hairs are on the leaves and stem; the latter being hollow except at the nodes. The broad leaves are once ternate and may exceed 15 in wide, and the petiole is distinctively inflated. The inflorescence of this aromatic plant is a compound umbel.

The genus name _Heracleum_ most likely refers to Hercules (Abrams 1951, Hitchcock et al. 1971) while the specific epithet, _lanatum_, describes the wooly pubescence found on parts of foliage and stalk. The species is a member of the Apiaceae (parsley or carrot family), formerly called the Umbelliferae. The genus has about 60 species in the Northern Hemisphere, but this is the only species native to North America. The type locality is in Canada. The distribution in North America extends from Alaska to Newfoundland and south to California, Arizona and Georgia. The species also is found in Siberia and the Kurile Islands. Moss and Packer (1983) described the distributional limits of this coarse perennial herb in the north as southern Alaska, Yukon, Hudson Bay and Newfoundland while the southern limits are California, New Mexico, Kansas, Ohio and Georgia; the species is also present in East Asia.

H. lanatum occurs abundantly within a wide elevational gradient from sea level to high mountains. Sampson (1924) identified the common habitats as open woodlands, shrub types and moist meadows with elevations ranging up to 9,000 ft. (However, one stand in his study with *H. lanatum* present was at 10,000 ft.) This species favors habitats in the moist shade, transition, and boreal zones (Abrams 1951).

Phenology

Onset of Growth-- *H. lanatum* begins to grow early in the spring and quickly produces abundant amounts of biomass. This trait is made possible because of the carbohydrates stored in the roots during the previous growing season. Considerable variation occurs in the actual time when growth begins depending on location of the population in terms of latitude, elevation and aspect. However, even at the same site, the date that growth begins may vary as much as a month from year to year depending on fluctuations in weather patterns. Carriles (1990) studied the phenology of H. lanatum and several other species important in bear habitats in the North Fork of the Flathead River. For the 4 plots with H. lanatum, the dates between years that growth began varied as much as 3 to 4 weeks. In fact, this species grew over 6 in tall under 2 ft of snow, and bears were digging through the snow to feed on the new shoots.

Flowering-- Time of flowering may vary over several weeks but occurs most commonly during a 4-week period beginning in mid-June. Most species of umbels have 200-300 different species of insect pollinators, and because of the array of different pollinating insects, are considered to be 'promiscuous' plants (Bell 1971). H. lanatum is quite typical of the family in this respect. The flowers are pollinated 50% of the time by Diptera (flies, mosquitoes and gnats) and another 25% by bees, wasps and ants of the Hemiptera.

Seed-- Generally, seeds mature in 6 to 8 weeks after flowering and pollination. In Iowa the seed are usually dispersed from late June to mid-July (Hendrix 1984). However, in my study area, the seed are shed from late July to early September. I have observed that flowers and fruits may deteriorate and not yield viable seed if the weather is rainy and cool and fungus begins to grow on the inflorescence.

Regrowth-- After the seeds are mature, the leaves wither and the large hollow stalk begins to dry and cure. Regrowth in the form of new basal leaves often occurs in the fall. This may be keyed to moisture availability. In certain years, if the soil is moist and the temperatures suitable for plant growth, it is possible to observe a new flush of vegetative regrowth from the root crown (Carriles 1990). The leaves may grow 1 to 2 ft tall. This phenomenon allows the plant to store additional carbohydrate reserves in the roots to aid in the flush of early growth the following spring.

Response to Disturbance

Zager (1980) found *H. lanatum* to be an increaser (based on a positive change in canopy cover) in old burns, scarified clearcuts, unscarified clearcuts and snowchutes. Since this species usually occurred in moist areas, he felt it would seldom be required to respond to wildfire or the impacts of timber harvests. This species may benefit when the tree canopy is opened and/or when logging activites alter the moisture regime.

Habitat and Community Type Classifications

H. lanatum is not a common species in forest habitat type classifications for the Northern Rocky Mountains. In the classification for Montana, *H. lanatum* was present on 39 of about 1,500 stands with an average cover of 1% and a low fidelity because the stands were members of 17 different habitat types (Pfister et al. 1977). Sampling was from late successional stages (late seral to near climax) which represented a range of environments but did not include earlier successional stages where *H. lanatum* may have been a major seral species. *H. lanatum* was not shown in the lists of common species for several other classifications that cover the areas of Idaho, western Wyoming, and northern Utah (Steele et al. 1981, Steele et al. 1983, Mauk and Henderson 1984, Cooper et al. 1987). Youngblood and Mauk (1985) had *H. lanatum* on 10 of 720 stands in 3 of 37 habitat types that averaged 3% cover for the forests of central and southern Utah. I suggest that it would be atypical for *H. lanatum* to be abundant, especially in areas larger than 0.25 acres in forest stands with a mature conifer canopy.

H. lanatum is a more important component of the understory in many *Populus tremuloides* stands. This species occurred in about 85 of over 2,100 stands on the national forests of the Intermountain Region and, in those stands, averaged 9% cover (Mueggler 1988). The stands were in 16 of 59 *P. tremuloides* community types. However, Mueggler and Stewart (1980) did not include *H. lanatum* in the classification for the shrublands and grasslands of Montana.

A study of the grizzly bear habitats in the Bob Marshall Wilderness found that *H. lanatum* occurred mostly in the cool and moist vegetation types (Mace 1984, 1986; Mace and Bissell 1986). Within the avalanche chute complex, H. lanatum averaged 6% cover as it occurred in 50% of over 180 streamside and Alnus shrubfield stands; the species also occurred in 40% of the mesic herbaceous fans in the same complex. It occurred in 31% of the tallgrass/Senecio triangularis type of the subalpine meadow complex. In the timbered creekbottom complex, H. lanatum was present in nearly 50% of the sites, both in timbered and glade openings surrounded by timber. Also, it was present in several types of the floodplain complex: Salix flat (73%), riparian Picea (63%), mesic herbaceous meadow (62%) and Populus trichocarpa (25%).

Other studies reported that H. lanatum grew well in riparian zones. Singer (1978) stated that it occurred in mesic sites where silt and nutrients were deposited. Based on a study of the bottomland hardwood forests in western Montana, Foote (1965) indicated that H. lanatum was one of a dozen of the most common forb species in the tributary stands. Boggs et al. (1990) specifically mentioned H. lanatum in the description of 5 types in the riparian communities of northwestern Montana with the following constancies and mean coverages: P. tremuloides/Calamagrostis canadensis habitat type (50% / 12%, n=4); Salix geyeriana/C. canadensis habitat type (45% / 4%, n=32); S. geyeriana/Poa pratensis community type (53%, 2%, n=24); and Alnus sinuata community type (80%, 2%, n=5). Specific values were not reported for H. lanatum in the Alnus incana community type but it was mentioned as a common forb for the type. Although the constancies were high for H. lanatum, cover values were generally low. The most cover for this species on a single plot was 25%, and then only on 3 plots.

Utilization by Man and Animal

Animals

Many species in the Apiaceae are important foods for man and animal, and this species is recognized by stockmen as a valuable pasture plant. Sampson (1924) indicated it is eaten ravenously by cattle, sheep and goats. First the leaves and flowers are eaten and then the juicy stem. For sheep and goats, H. lanatum is considered an excellent forage and highly relished during most of the season when available. Rated a good forage for cattle, it is also relished during most of the season when available. Not all animals prefer it; for horses, which do not use it much, the forage rating is only fair. However, all factors considered, H. lanatum is considered a good forage, but it was not an abundant forage crop in Sampson's studies. H. lanatum provides excellent forage for game and livestock (Plummer et al. 1955). Cattle are particularly fond of it; hence the common name cow parsnip. Because of its recognized palatability, areas that have seedlings and young plants just beginning to establish should not be grazed or if grazed then only lightly (Plummer et al. 1968).

An extensive study was made of the subalpine vegetation of the Wasatch Plateau in central Utah by Ellison (1954). This involved 6 relic natural areas that had not previously been grazed by domestic livestock or only lightly in the many years preceeding. He reported the following: "One of the most striking things about these natural areas is the abundance of species of perennial forbs and the large proportion they make of the total vegetation....Another outstanding fact, besides the varied mixture of forbs and grasses, is the number of species that are scarce on heavily grazed range except as relics growing in spots protected, or partly protected, from grazing....*Heracleum* *lanatum* ... is only rarely found in the subalpine zone today, even as a relic, probably because the protection given by thickets of shrubs is inadequate for a plant so large and highly palatable." The original upland-herb associations, he felt, were comprised of many species of tall, succulent forbs, grasses and sedges. *H. lanatum* was probably one of about 16 prominent species; however, seldom would a single species dominate extensive areas.

Armitage (1979) studied the food selectivity of yellow-bellied marmots. Other researchers had previously stated that *H. lanatum* is "sweet" and eaten readily by big game and domestic animals. In this study, the yellow-bellied marmots preferred the diet of this plant over seven other species.

H. lanatum is important in the diets of both grizzly and black bears. Tisch (1961) studied the seasonal diets of black bear in the Whitefish Range of northwestern Montana. *H. lanatum* was the most heavily utilized forb in their food habits. In the spring, primarily leaves comprised the diet; by late June and through July, use of large stems had the highest occurrence. A study of the grazing food habits of grizzly bears was conducted in mesic habitats of wet meadow, aspen and willow in morainal drainages of the North Fork of the Flathead River. Singer (1978) reported that *H. lanatum* occurred on 8 of 26 feeding sites, more than any other plant species that the bears ate, and the bears utilized the plants during succulent stages. Mace (1984) reported on grizzly bear habitats in the Bob Marshall Wilderness. Preference for _H. lanatum_ vegetation ranked high and was considered a "key" succulent food. Two reports give the results of a food habits study of bears in Glacier National Park (Kendall 1986, Martinka and Kendall 1986). Over 1500 fecal samples were collected between 1967-71 and 1982-85 and analyzed for different types of food. The results were reported in the frequency and volume of use by season. Over 90% of the year-long diet volume was comprised of vegetation: about 60% leaves, stems and roots and 30% berries and fruits. Kendall (1986) showed that _H. lanatum_ was the most important herb in the bears' diet and provided 15% of the total volume consumed annually (Fig. 1). But more importantly, the bears' consumption of _H. lanatum_ was not seasonally uniform. For the same years as above, the frequency of occurrence in the scats and the percent of total volume were respectively: spring (13% / 9%), summer (41% / 34%), late summer (8% / 6%), and fall (6% / 4%). Also, for the summers of 1984 and 1985, _H. lanatum_ averaged to comprise 43% of the volume of the total diet.

Little information exits about the nutritional value of _H. lanatum_. However, Sizemore (1980) reported the nutritive content of a dozen plant species important as bear foods in the South Fork of the Flathead River study area in northwestern Montana. The information for _H. lanatum_ is given in Table 1. Of the 12 plant species analyzed, _H. lanatum_ had the highest percent protein, relatively high percentages of fat, moderately low percent available carbohydrates, moderately high nutritional availability index, and moderately high values for the percent cell content.

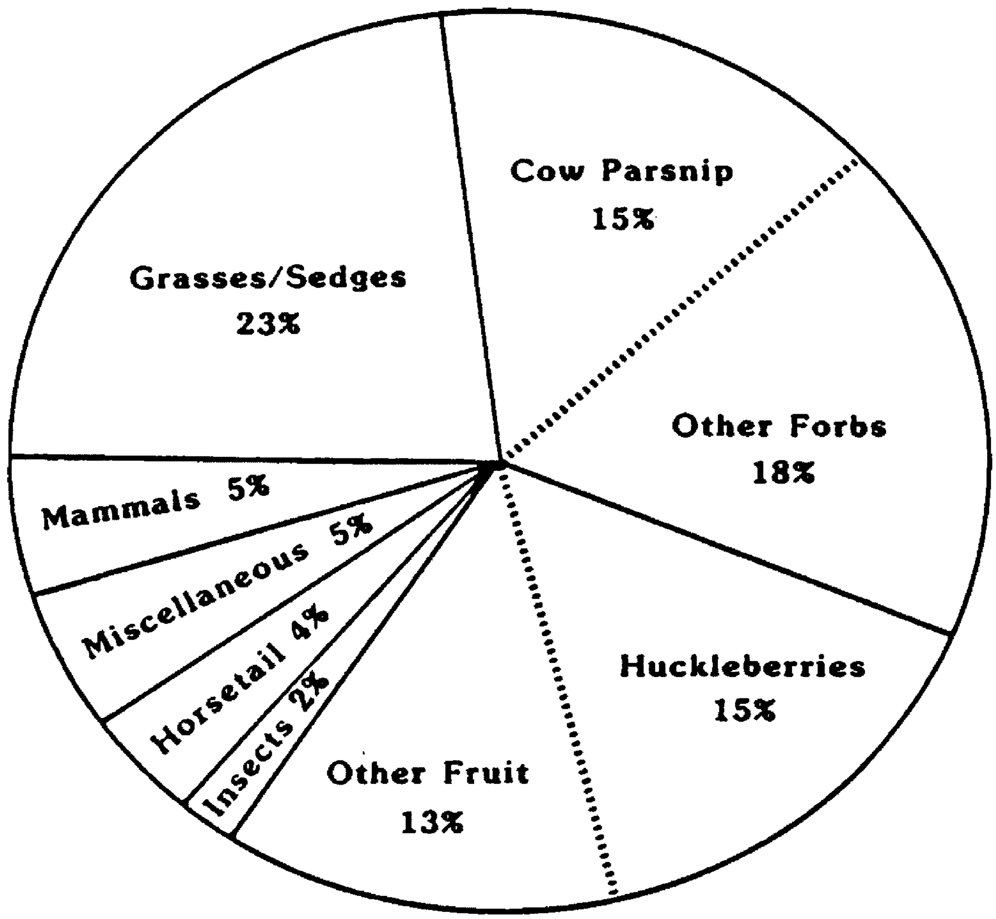

Fig. 1. Major food classes comprising the total diet volume of bears in Glacier National Park. Determined by fecal analysis, 1967-71 and 1982-85 (n=1514) (Kendall 1986).

Table 1. Average chemical composition of *H. lanatum* 1/ (Sizemore 1980).

Species	Description of Plant 2/	Protein	Fat	Available Carbohydrates	NAI 3/	CW-CC 4/
		----------Percent----------				--Percent--
H. lanatum	1',cp,nf	28.7	5.92	4.40	1.59	22.52-77.48
	2.5',cp,nf	27.2	6.82	5.19	1.60	22.96-77.04
	4',cp,ef,if	20.7	5.45	3.97	1.17	48.07-51.93
	4',f,if	28.8	8.35	5.00	1.78	25.93-74.07

1. multiple samples and chemical analysis trials
2. numbers - height of plant, cp - complete plant, f - flowers, if - in flower, ef - except flowers, and nf - not in flower (assumed)
3. NAI - nutritional availability index
4. CW - cell wall, CC - cell content

Use by Native Americans

H. lanatum was used by several of the Indian tribes of North America. Hart (1974) gives detailed information about the ethnobotany of the Salish and Kootenai Indians of northwestern Montana, who occupied most of my study area. The Kootenai ate the young stems; however, the Salish probably used the species more extensively. In addition to commonly eating the peeled young stems raw as greens, the Salish often used the mature and dried hollow stems to make elk whistles. As a medicinal use, they would prepare a poultice from either fresh or dried roots which was applied to swellings, especially of the feet. However, there was not any mention that the roots were used as a food.

The marrow and root of this species have sugar and a licorice flavor. Some Alaskan tribes eat the marrow raw and boil the roots (Hulten 1968). French (1971) provides a comprehensive treatment of the ethnobotany of the Umbelliferae and reports several uses of *H. lanatum* by many Indian groups of the United States and Canada, including the Eskimos. The stems, petioles, and leaves are edible, and occasionally the roots were also cooked and eaten. The roots are also reported to be a source of dye, but I do not know for what color. The plant was used as a medicine for the Plains Indians and the early white settlers in the Midwest, and several of the tribes also had ceremonial uses. Of H. lanatum he stated, "considering food, medicine, and ceremonies, this was probably the most widely used native Umbel in North America."

Several members of the Apiaceae are edible, but others are poisonous, some deadly. Two species, Cicuta douglasii (water-hemlock) and Conium maculatum (poison-hemlock), are deadly poisonous and have some features similar to H. lanatum. French (1971) cautioned people to avoid trying any species in this family that they do not know well.

Given the multiple and diverse uses of H. lanatum, it should not be too surprising that the literature is replete with tidbits of information. In fact, H. lanatum might well be considered the "Trivia Plant of the Northwest." At the same time it is ironic that much of the information in print about this species is contradictory; some is erroneous.

Misunderstandings, Misconceptions and Misinformation

Some of the early references about this species attributed facts to this plant which are not correct. Unfortunately, many of these misconceptions are still in vogue. The following quote comes from a more recent description of Cow parsnip, Heracleum lanatum (Michx.), Apiaceae (Parsley family) (Whitson 1987): "This introduced biennial from Europe reproduces by seed, forming a low-growing rosette its first year with large, fleshy taproot. Flower stalks grow 2-4 feet tall. Stems are somewhat hairy and grooved. Leaves are glabrous, once pinnately-compound with serrated edges, not carrotlike. Cream colored flowers form with five petals in umbels at the top of short stalks. Flower clusters are mostly flattened with outside flower stalks curving inward with maturity. Seed is flattened on one side, rounded on the other, with distinct ridges."

"Cow parsnip occurs mostly in disturbed areas and along roadways. It now inhabits many sites in intermountain regions, frequenting drier sites. Its genus name means parsnip in Latin."

Two captions are also provided for the pictures that accompany the description. "Leaves, commonly 6-10 inches across, are deeply divided, not pinnately compound like other parsley family plants that are poisonous." And, "Cow parsnip has flat-topped umbel flowers which resemble poisonous plants in this family."

My intent in using this example is not to be critical but rather to point out several of the misconceptions still circulating about this species.

Based on my field observations and general information in the literature, I would describe the species in their format as follows. This long-lived perennial is native to North America and reproduces by seed. Growth for the first few years is slow with one to a few simple leaves. The taproot remains small for a couple of years and later becomes fleshy. As plants mature, a type of fleshy fibrous root system generally develops along with the fleshy taproot. Flower stalks grow

2-10 feet tall. Stems are slightly grooved and glabrous to somewhat hairy, especially at the nodes toward the top. Leaves are glabrous to generally pubescent particularly beneath, once triternately compound, and the lobed leaflets have serrate margins. The inflorescence consists of one to several compound umbels each borne on stalks up to 3 feet long. The flowers are white and each has 5 deeply cleft petals. Two seeds are borne together on a filament-like stalk. The inner side is flat with 2 distinct oil tubes and the outer seed surface is flat to slightly rounded with 4 oil tubes visible.

H. lanatum grows commonly in disturbed areas that receive additional moisture during the year. Streamsides and moist sites along roadways are common habitats. The species is widespread in the intermountain regions, but has decreased in the past several decades because it is a highly palatable species that does not withstand heavy grazing pressure. In various forms of Greek and Latin, the genus name refers to Hercules, god of physical strength.

The triternate leaves do not resemble the compound leaves of the poisonous members of the parsley family. Each of the 3 leaflets is deeply divided, and the leaf is often 12-20(24) inches wide. The flat-topped umbel of flowers might be mistaken for some of the poisonous plants in the same family.

Recommendations for Propagation

Several managers and biologists have expressed interest during the past few years in propagation of *H. lanatum*. The interest is widespread and comes from several national forests in two regions, as well as the Bureau of Land Management and two national parks.

Historical Cycle

The value of *H. lanatum* as an excellent forage for animals has been recognized for at least 67 years (Sampson 1924). The notion of propagating *H. lanatum* is an old idea that has been around for nearly 55 years. This underscores the value of completing a thorough literature review to have the benefit of the experience of others who have worked on similar problems. The recommendations for propagating this species were mentioned in the late-1930's, the early-1950's, the late 1960's and the mid-1980's. Some of the information that follows was also briefly summarized by Redente et al. (1982).

In the late 1930's some attention turned to the culture and protection of lesser vegetation in the forests of California. This information was later redistributed by the Civilian Conservation Corps and also incorporated in recommendations from the Soil Conservation Service about the propagation of trees, shrubs and forbs (Mirov and Kraebel 1937, 1939; Swingle 1939). *H. lanatum* was credited with the following characteristics: time of seed collection was from July to September, there were approximately 76,000 seeds/lb, no treatment was required for germination, there were 32 days between sowing and germination, and the highest germination rate was 39%.

The earliest work to actually plant and study the growth of *H. lanatum* in a variety of controlled field conditions began in 1950. Ellison and Houston (1958) selected 4 general sites in the continuous *P. tremuloides* zone with elevations ranging from 8,050 to 9,000 ft in

Ephraim Canyon of central Utah. At each site 9 plots, 10 ft square, were established. Six plots were paired and located under the P. tremuloides canopy while the other three plots were situated in openings 25 to 75 ft from the edge of the trees. One plot from each of the three pairs had a trench 18 in deep dug around the perimeter to sever the roots from adjacent aspen and shrubs. Thus, 3 treatments (full sun, shaded under P. tremuloides canopy, and trenched/shaded under P. tremuloides canopy to remove competition for water) were replicated 3 times at each of 4 sites for a total of 36 plots.

All plots were spaded and each was divided into 4 subplots 5 ft square. Each subplot was seeded with one of the species, Bromus carinatus, Elymus glaucus, Rudbeckia occidentalis or H. lanatum, such that each of the species was seeded in each of the 36 plots. The plots were seeded with about 2 seeds per inch of row in the fall of 1950. In 1951 all the stands were thinned to one plant per 2 inches of row and the bare spots reseeded in the fall. Plantings were weeded regularly. B. carinatus was consistently the most successful, and H. lanatum the least successful.

None of the subplots of H. lanatum in the open produced a full stand; in fact, 8 of the 12 open plots did not have any H. lanatum after 3 years. However, the few H. lanatum plants on the remaining 4 plots (all at the lower elevations) were relatively large and thriving. The authors suggested that the lack of this species in the open plots may have resulted from an inability of the seedlings to become established in the open at the higher elevations. Once the plants became established, growth resulted possibly because of reduced competition.

After 3 growing seasons, the H. lanatum on the trenched plots had a 10-fold increase in yield over the untrenched plots under aspen. This increase occurred in 2 ways: size of the plants and numbers of plants. The trenched plots had an average of 59 plants which averaged 13 cm tall. Untrenched plots only had an average of 33 plants per plot with an average height of 6 cm. A photo of one untrenched plot after 6 growing seasons showed possibly two dozen plants, but all appeared to be less than a foot tall. The advantages of H. lanatum growing under a P. tremuloides canopy is greater atmospheric humidity and more fertile top soil. The advantage provided for open-grown H. lanatum is more light and more moisture as a result of less aspen competition. This might be the most significant reference of the entire literature review. H. lanatum does not establish easily and once established its development is extremely slow!

A major handbook of recommendations for seeding rangelands in Utah, Nevada, southern Idaho and western Wyoming provided minor details and general suggestions for the use of H. lanatum in rangeland improvement (Plummer et al. 1955). It is a native perennial that is well adapted for seeding in mountain lands and grows well in the shade. The species is slow to establish but once established, reseeds effectively. Establishment occurs best where an overstory or brush mulch exists to protect the seedlings from drying out or frost. It is a good species to seed in moist areas of the mountain brush zone, subalpine ranges, and particularly under P. tremuloides, but it has restricted value in areas other than these specifically mentioned. Seed might be included in mixes for either well-drained or moist soils. They recommended this forb for general use in shaded sites under tall brush or P. tremuloides and to a lesser extent in openings in Pseudotsuga menziesii or Picea engelmannii stands.

More than a decade later, additional recommendations became available for the use of H. lanatum in the restoration of big game range in Utah. It is a good species to seed in the aspen and associated conifer types (subalpine) with the implication that it is strongly shade tolerant (Plummer et al. 1968). Also, mountain brush communities and wet meadows have some selected areas suitable for planting H. lanatum as a special use species. They gave the following characteristics for the seed: maturity occurs between August 15 and September 10, there are 44,850 seeds per lb, 90% purity is acceptable, and seed collected by hand from wildland stands was worth $.60/lb in 1968.

A table in their handbook listed the relative value of H. lanatum on a scale from 1 to 5 (very poor to very good) in 20 different attributes. Ranges of adaptation and initial establishment were considered poor. The following were listed as fair: growth rate, persistence, seed production and handling, natural spread, availability of current growth, tolerance to grazing, resistance to disease and insects, edible foliage retained in fall and winter, and ease of transplanting. These are the values that rated good: final establishment, germination, ease of planting, herbage yield, soil stability, compatibility with other plants, palatable early spring growth, and palatable summer growth. They rated overall palatability as very good. I do not know how these traits were defined and if all of the information was from actual experience or if some information was given as "considered opinion" for certain species. For example, I do not know if there had actually been work done with transplanting this species. H. lanatum was given a composite suitability index of 68%; for all forbs the suitability index ranged from 63 to 87 with most in the high 60's or low 70's.

There did seem to be some minor inconsistencies in the information given relating to palatability, suggested seeding rates and areas where H. lanatum is most adaptable. However, this was general information given for more than 130 species and a dozen major types of vegetation and sites.

Seeding rates for H. lanatum in the seed mix was given as 1 lb/a for P. tremuloides and associated conifers in the shade, but not included for the open areas. For the subalpine herblands and P. tremuloides openings this species was not recommended on well-drained soil, but for moist soils 1 lb/a for broadcast seeding and 0.5 lb/a in the seed mix if drilled. Specific seeding rates for H. lanatum were not mentioned in the text for the mountain brush or wet meadow types. General recommendations for use of all seed mixes in range restoration stressed the value of fall plantings. In the spring it is hard to seed large areas after the snow melt but before it becomes too dry to plant. Also, the seeds of many shrubs and herbs have dormancy requirements that are naturally broken during the winter. Such seed will not germinate if planted in the spring unless the seed were specially treated to break dormancy. After areas are seeded by hand or from aircraft, it is helpful to cover the seed. This may be done with livestock grazing or even the "milling" of livestock through the seeded area can help.

Seed Collection and Germination

Because of the interest of establishing *H. lanatum* in new areas, attention focuses on the seeds, methods of collection, and germinative capacity. Vegetative propagation of *H. lanatum* is unknown (Hendrix 1984), but I suggest that this is because such attempts have not been documented.

Seeds-- The fruit of *H. lanatum* is a dry schizocarp formed by two flat mericarps that are each obovate to obcordate (Hitchcock et al. 1971). Each mericarp has four distinctive oil tubes on the dorsal (outer) surface and two oil tubes on the ventral side.

Collection-- The seed may be collected by hand stripping the seeds from the umbels directly into a container (Plummer et al. 1968). It was suggested to dry the seeds and clean them with a fan prior to storing. Duration of good viability was reported for up to three years.

Germination-- At least four independent studies provide information about germinating *H. lanatum* seed. Researchers in California reported 39% germination and indicated that no treatment (including stratification) was required (Mirov and Kraebel 1937, 1939; Swingle 1939). Another study was done on the germination of *H. sphondylium* (I consider this to be synonymous with *H. lanatum*) seeds collected in northwestern Colorado. Hoffman (1985) reported 8% germination and stressed that this species germinated only in light. The study had 14 different treatments: combinations that varied the amount of stratification from 0 to 120 days, light or dark, and temperature variations from 2 to 24 degrees C. Following stratification for 120 days, the treatment where seeds were placed in the light for 20 days with daily temperature fluctuations of 16 hr of 24 degrees C and 8 hr of 2 degrees C was the only treatment where any of the Heracleum seed germinated; germination was only 8%. This information may suggest that different ecotypes occur for this species. Some of the ecotypes may not require a period of stratification to break dormancy. There may also be a critical ripening period in the field before the seeds should be collected.

McDonough (1969) studied seed collected in northern Utah and reported that stratification may be required for many species on mountain rangeland. If a species does not respond to photoperiod, alternating temperatures, scarification, leaching or removal of accessory parts, then stratification for 3 to 4 months in water or GA3 (gibberellic acid) may break the dormancy. In his study, cleaned seeds were stored in vapor-tight bottles at 2 degrees C. Tests were made on duplicate dishes of 50 seeds each and then repeated once. First the seeds of this species were imbibed in water and incubated for 28 days at 8 hrs light and 16 hrs dark with average illumination of 50 lux. Temperatures alternate with the light regime. Germination for 32/22 and 22/17 degrees C was 0%; for 17/12 degrees C, 1% germinated. However, when H. lanatum seed was stratified 16 weeks at 2 degrees C, germination was 28% in water and 34% in GA3. But when the temperature following stratification was 22/17 degrees C, 96% of those in water germinated (3 days) and in GA3 93% (4 days). The number of days was the time to reach half the final germination percentage. GA3-imbibed seed did not germinate at significantly higher rates. H. lanatum appeared to contain a leachable substance that was removed by washing the seed 4 hours in running tap water. He did not test to see if the leachate inhibited germination. This study demonstrated that *H. lanatum* may have a high germinative capacity following a stratification period of 16 weeks.

One other study considered the effect of acid scarification from passing through a bear's digestive tract on the germination rate of *H. lanatum* seed. Applegate et al. (1979) compared 150 seed collected from 6 bear scats (possibly the same bear) with 150 control seeds. Half of the seeds in each group were frozen overwinter; the remainder were kept in a refrigerator. In the spring, all of the seeds were placed in a growth chamber in wet sand with daily fluctuations of temperature and light comparable to those of Glacier National Park. The control seeds for the frozen and unfrozen treatments germinated at 69% and 51%, respectively. Seeds collected from the scats germinated at significantly higher rates: 85% for the frozen and 65% for the unfrozen treatments.

Research Needs

Grizzly Bear Habitat Research Needs

Jonkel and Hadden (1986) ranked 10 needs for grizzly bear research by priority. The top four related directly to the current lack of knowledge about the ecological life history of *H. lanatum*. The first need pertained to studies of disturbed site vegetation. *H. lanatum* was identified as a prominent member of communities along flood plains, river banks and creek bottoms. The second need centered on habitat improvement because vegetation recovers slowly on some disturbed sites. What ways can be used to improve disturbed sites and accelerate habitat recovery through the propagation of bear foods? The third priority dealt with high-density grizzly complexes and the need for management of these areas. Bears are attracted to H. lanatum communities, especially in June (Hadden et al. 1986). Species-specific vegetation studies for key bear foods was the fourth need; H. lanatum was the first species listed. They suggested that this species is a well-known plant, but its autecology is not sufficiently understood for the purposes of bear habitat management.

Weaver (1985) indicated that a scarcity of information exits about the biogeography and autecology of many plant species, including H. lanatum, that are important in grizzly bear diets. Several research topics were listed that would provide useful information about these species: what conditions influence the abundance and distribution, how much variation occurs in production and what is the response to fire, logging and grazing?

Vegetation Study Methods

Plot Location

An important decision in a vegetation study is to determine the method of selecting the sample or plot. Mueller-Dombois and Ellenberg (1974) suggested the releve method to locate the plot. With this approach the process of entitation is important. This relates to the ability to recognize distinct entities in the vegetation cover. Another important concept they discussed is that of homogeneity where plant cover should be as homogeneous as possible. Also, the habitat should be uniform within the stand area. Pfister et al. (1977), Youngblood and

Mueggler (1981), Mattson (1984), Youngblood et al. (1985) and Mueggler (1988) all used this method of plot selection.

Plot Size and Shape

H. lanatum often grows in small stands and in riparian habitats. Consequently, large plot sizes may include ecotones and areas within the plot where H. lanatum does not grow. Mattson (1984), Youngblood et al. (1985) and Platts et al. (1987) all used a 5 m X 10 m plot or occasionally a 2.5 m X 20 m plot and thus retained the uniform plot size. This size and configuration is recommended to sample most riparian stands. Kessell (1979) used several plot sizes and shapes, but the 5 m X 10 m plot was one size used for stands similar in structure to those with H. lanatum. Cook and Stubbendieck (1986) pointed out that when vegetation is sparse and appears in clumps, the rectangular shaped plot may be most appropriate.

Cover Estimates

Two different approaches are used to estimate the amount of aerial cover by species on a plot. Cover may be recorded in cover classes (Pfister et al. 1977) or estimated in absolute values (Mueggler 1988). Bratton (1976) used a scale of estimated percentage cover values: 1, 2, 3, 4, 5, 6, 8, 10, 12, 15, 20 and continued to 100 in 5% increments.

Classification, Direct Gradient Analysis and Ordination

Gauch (1982) explained that vegetation ecologists often use a triad of methods to organize their data. This triad includes classification, direct gradient analysis and ordination. Such an approach is useful for description, discussion, understanding and management of communities. He contrasts these methods: classification and ordination use only species abundances to organize the data while direct gradient analysis makes use of recognized environmental gradients. He further explains that all three methods are complementary.

During the past decade and a half, researchers completed several vegetation classifications including four for Montana. Pfister et al. (1977) and Mueggler and Stewart (1980) classified habitat types in Montana based on the potential for sites to have similar climax vegetation. Often, however, climax vegetation may not presently occupy the site. Boggs et al. (1990) only classified part of the riparian and wetland sites as habitat types considered to be climax. The remainder of their sites were classified as community types. Arno et al. (1985) developed a classification for successional forest community types within the logical framework of forest habitat types.

Other studies have classified community types based on existing vegetation without the presumption of climax (Youngblood and Mueggler 1981, Youngblood et al. 1985, Mueggler 1988, Boggs et al. 1990). The structure and composition of existing vegetation determine the community type without regard for temporal scale or successional status (pioneer, seral or climax). Thus, community types are the units of vegetation that resource managers may deal with on a day-to-day basis.

Mueller-Dombois and Ellenberg (1974) described the methods used to classify communities. These methods rely on the presence and abundance of species in the community. Typically, this involves making a species list for the community and recording the percent canopy cover for each species. These methods use species in the plant community as integrators of the environmental conditions.

STUDY AREA AND METHODS

Description of Study Area

Location

All the field work for this study was done in northwestern Montana west of the Continental Divide (Fig. 2). The southern extension of the study area is Lolo Pass about 35 miles southwest of Missoula. The western extension is near the Ross Creek Giant Cedars scenic area. The northern limits of the study area extend from Loon Lake about 10 miles north of Libby in the west to Logan Creek near Logan Pass in Glacier National Park on the east. The northern most extension of the study area is Hay Creek in the North Fork of the Flathead River drainage about 5 miles northwest of Polebridge. The eastern limit is Marias Pass on the Continental Divide some 25 miles southwest of Browning. In all the study area is about 120 miles from east to west by about 150 miles from north to south.

The 49 releves were not randomly located nor evenly distributed in the study area. Rather, the plots were paired or clustered in groups of 2 to 8 in 12 different general areas. Each general area is restricted to approximately a 5-mile radius although several areas are much smaller; the smallest has only a 25-meter radius. Five general areas are on the Flathead National Forest: Hay Creek northwest of Polebridge (4 plots), Martin Creek northwest of Kalispell (2 plots), Lost Johnny Creek west of Hungry Horse Reservoir (4 plots), Marias Pass/Granite Creek vicinity (4 plots) and South Fork of Lost Creek near Swan Lake (3 plots). Two general areas are in Glacier National Park: Fish Creek

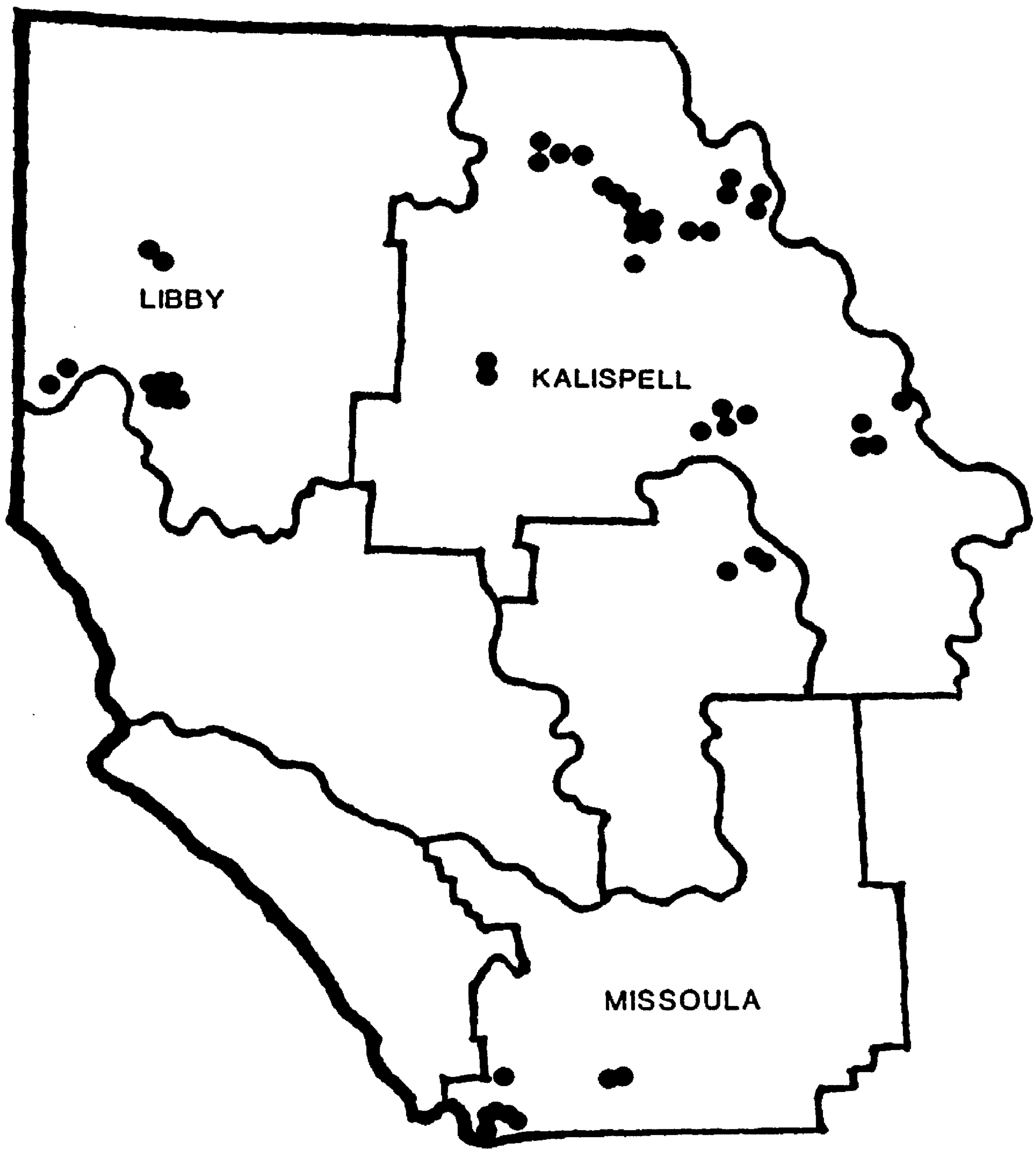

Fig. 2. Map of the study area with general location of the 49 releves.

Campground to Lone Pine Prairie south of Polebridge (8 plots) and Going-to-the-Sun Highway from Avalanche Creek nearly to Logan Pass (6 plots). There were three general areas on the Kootenai National Forest: Loon Lake north of Libby (2 plots), Ross Creek and Bull Lake south of Troy (2 plots) and Bear Creek south of Libby (6 plots). The final two general areas were on the Lolo National Forest: lower Lolo Creek (2 plots) and upper Lolo Creek (8 plots). Elevations for the releves range from 2,200 feet to 6,000 feet.

Geology and Soils

Parent materials in most of the general areas derived from Precambrian upper or lower Belt sediments (Alt and Hyndman 1986). Exceptions include: 1)sandstones and shales from the Mesozoic in the Marias Pass/Granite Creek area, 2)Tertiary basin fill in the west portion of Glacier National Park where releves were located from near Fish Creek Campground to Lone Pine Prairie, 3)sand and gravel from the Pleistocene at Bull Lake, and 4)the Tertiary Lolo granite batholith west of Lolo Hot Springs. Parent materials for most of the releves were disturbed formations, often unconsolidated and generally depositional (e.g., riparian flood plains, toe slopes of avalanche chutes or glacial moraines and blanket deposits).

For the 35 releves located on national forest land, Land System Inventory maps were used to identify land type and the associated soil classification and landform (Martinson and Basko 1983, Kuennen and Gerhardt 1984, Sasich and Lamotte-Hagen 1989). The soils occurred in these general areas: Aquents and Fluvents in the flood plains, Cryocrepts and Orthents along stream bottoms, Andeptic Cryoboralfs and Dystric Cryochrepts on ground moraines, Boralfs and Ochrepts on glacial troughwalls, and Andic Cryochrepts on glacial tills. These are mostly young soils of depositional origin in addition to the influence of loess from volcanic ash. Subsoils are often stratified with silts, sands and gravels and have seasonally high water tables. These soils belong to the orders Entisols, Inceptisols or Alfisols. Buol et al. (1980) generalize these soils respectively: recently formed, embryonic with few diagnostic characteristics, and soils of the temperate region that have more clay in the B horizon than in the A horizon. Soils of limestone origin are not common in the area; none of the plots were considered to have soils with calcium/magnesium carbonate abundant in the substrate.

Climate, Precipitation and Riparian Influences

The entire study area is within the same general climatic regime influenced by a maritime weather pattern. Throughout the study area precipitation varies from about 15 inches per year in the lower Lolo Creek drainage (NOAA 1987) to 80 inches per year near Logan Pass (Finklin 1986). Much of this moisture accumulates in winter as snow, and in the northern portion of the study area substantial amounts of snow fall most years. It is significant that most of the areas sampled were considered riparian and received additional amounts of moisture during the year, particularly in spring. This increased moisture may come from nearby streams, the deposition zone of avalanche chutes, from springs, seeps and perched water tables particularly in the forested areas or clearings and openings surrounded by forests.

Field Methods

Integrator Concept

The following analogy illustrates the concept of an environmental integrator. Suppose it were possible to purchase a sensitive field instrument that, when placed in a plant community, could measure precisely all of the environmental factors which influence that site. But even more importantly, the device could measure all of the interactions among all of the factors. Now suppose that not only is that instrument available, but in fact, there are dozens of such instruments to choose from, each with varying degrees of precision and calibrated for different segments of the range for each environmental gradient. A plant species is comparable to such a device and is an integrator of the environment. Thus, a specific plant or a group of plant species growing at a site can be used to characterize a particular environment. Certain species may have narrow environmental tolerances while some others have broad ecological amplitudes.

The Releve

Consistent with numerous other vegetation studies, particularly type classification studies, I used the releve method of plot selection (Mueller-Dumbois and Ellenberg 1974). In the context of this study, the terms plot, sample, and releve are synonymous. Stand, however, refers to the entire area including and surrounding the releve where *H. lanatum* was present and the vegetation was essentially uniform.

Reconnaissance

The easiest time of year to identify sites with high abundance of *H. lanatum* occurs roughly during a three-week period from mid-June to early July when the mature plants are in full bloom with their white flowers clustered in large compound umbels atop the 4 to 6 foot (or even taller) stalks. Concentrations of *H. lanatum* may be seen more than a half mile away. Prior to the start of sampling releves, I made a reconnaissance trip through the study area in late June and tentatively identified several general areas where plots could be located later in the summer. Biologists on some of the ranger districts and researchers in Glacier National Park were also helpful in directing me to certain general areas.

Also, from my travels during the previous two summers I had some ideas of drainages to visit and roads to travel to find *H. lanatum*. During the summer of 1986, I experimented with some field methods and located 11 *H. lanatum* releves. At that time I used circular plots, so I did not use any of the 1986 data. However, I did resample 9 of those same sites in 1987 with the standard sampling method described below.

Stand and Plot Selection

My objective was to identify and sample during the course of the summer stands that represented gradients for moisture, aspect, elevation, slope position, and abundance of *H. lanatum* as a function of cover of the mature plants. Generally, I drove along roads in areas where *H. lanatum* might occur, developed a sense for which locations seemed to provide the variation of situations where the species grew, and made notes of candidate stands. Then I selected the stand or cluster of stands that provided a good representation of the variation in that area. I usually selected stands that were visible from or within close walking distance of the road. Sometimes I decided immediately to sample an area based on the abundance of _H_. _lanatum_ and uniqueness of the area. In most cases the decision to sample a certain stand was made without a knowledge of the microsite features and understory species present.

When releves were paired or clustered together in the same general area, I always tried to find contrasting environmental conditions. I attempted to locate releves that were unique in one or several environmental factors or in species composition. Thus, as the summer progressed, I became more selective and ruled out certain populations because of my perception that they were similar to other stands that I had already sampled in that part of the study area. However, a population that was quite similar to a previous stand would be considered if the location was in a completely different part of the study area. Because populations at lower elevations mature earlier in the season, I generally concentrated my efforts at the lower elevations during most of July and gradually worked my way to higher elevations though August. Many of the plots at the lower elevations were located in stream bank habitats and later in the field season, more alvalanche chutes were sampled.

Only one criterion was required for plot selection: _H_. _lanatum_ must be growing on the site. As a rule of thumb, I looked for an area where individuals of the species were distributed over an area of at least 100 sq m. In addition, the plot was situated such that individuals in the population were also outside of the plot on at least 3 sides, preferably all 4 sides. As a way of reducing some personal bias, I made the decision to place a releve in a given area from the edge of the stand before I actually walked through it. This decision was based on obvious environmental factors and general composition of the cover species. The decision to sample there was made before I had seen any of the understory species, the abundance of seedling or young *H. lanatum*, the specific soil characteristics, or any other microsite features.

Once I decided from a distance to locate a plot in the stand, I would enter the stand and visually and subjectively integrate what I was seeing in terms of uniformity of the dominant vegetation and physical features of the site and place the range pole for the center position on the releve's baseline. Because I sampled each plot intensively, my "n" number for the study was low, and because I wanted samples from a variety of different types and gradients, I occasionally elected to not locate a plot there after entering the area. But that decision was made only if the location seemed to be quite similar to other releves already sampled in that particular forest. These decisions occurred primarily later in the season when I continued to seek new types of situations where *H. lanatum* grew, but I did not have represented in my previous samples. Once the decision was made to set up a releve, I competed the plot. The one exception to this approach occurred at Packers' Roost in Glacier National Park where I abandoned a plot because of the presence of a black bear.

Plot Orientation

Generally, I positioned the releve (5 x 10 m) so that the long axis was parallel to the stream's edge in or near riparian areas. This tended to minimize the effect of the moisture gradient that changes dramatically in relatively short distances away from the water's edge. In upland locations the plot's length was parallel to the contour or at right angles to the slope. Particularly on steeper slopes this gave a better perspective to view the vegetation from the baseline without trampling the plot excessively.

Setting Up the Plot

To choose the exact location for the plot, I walked through the area visually integrating the typical vegetation and micro-relief for the area of the population and tried to situate the plot to include a uniform representation of the general composition of the larger area of the population. The position of the range pole placed in the ground became the center of the 10-meter baseline. The baseline formed the releve's lower edge and ran parallel to the contour unless some unusual circumstance made it preferable to orient the plot differently. An optical tape measure and compass were used to locate the other 4 range poles that marked the corners of the 5 x 10 m plot. The two corners at the ends of the plot's baseline were marked by measuring 5 m back to the center pole on the baseline and aligning the three poles in a straight line. With the compass, I determined the bearing of the baseline and then went to the general location of each of the two corners at the top of the plot. With the compass, I found the line at each side of the plot that was perpendicular to the baseline at each end of the baseline. Next I used the optical tape to measure 5 m along the side line from each corner on the baseline to each corner at the top of the plot. Once the top corners were marked, I double checked the plot's dimensions and shape by measuring the distance (which should be 7.07 m) from both top corner range poles to the center pole on the baseline. Also, the compass bearing between the two top corner poles should be the same as the first bearing taken along the baseline.

Data Collection

Once the releve was marked with the 5 range poles, data collection proceeded in a systematic way. I took at least two pictures (35 mm slides) of each releve, one from each lower corner looking diagonally to the upper corner on the opposite side.

Site Description

I recorded the site name, plot number, date, ownership, topography, configuration, aspect (general), aspect (plot), percent slope and estimated area of the population of *H. lanatum*. I drew a brief diagram of the plot and its relationship to adjacent landmarks. I made descriptive comments about general observations, surrounding vegetation, *H. lanatum* growth form, wildlife use, livestock use, lateral distance to water, and a note about disease and insects. The plot location was marked on the forest map, and the township, range, section and quarter section were usually recorded. I wrote a brief narrative of how to locate the releve by use of local landmarks and distances from a paved highway. The plots were not permanently marked, but the description would help someone return to the specific stand of the releve if not to the exact location. Elevations were recorded later from topographic 7.5 min quadrangles at the University of Montana map collection.

Percent Canopy Cover

Up to this point I had generally refrained from walking onto the plot except to place the photo card with the plot number. I wanted to be careful not to trample the vegetation before making the cover estimates. Next, a species list was started for the plot with *H. lanatum* on the top and the forbs, shrubs, grasses and trees recorded in separate parts of the data sheet. The most obvious species were recorded first and estimates made of the cover while moving as little as possible to reduce trampling. Then a more concerted effort was made to find all the different understory species and those with trace abundance. Absolute cover rather than a cover class was recorded for each species. The 29 possible values were 1 to 10 by 1's, 12, 15 to 95 by 5's, and 98. Also, for each species I recorded sociability on a scale from 1 (singly) to 5 (great crowds).

My cover values were more refined than the broad cover classes used in many ecological studies. However, I used some rules of thumb and some mental images to visualize the vegetation in terms of percent cover. One rule was to divide by half. Is the cover greater or less than 50%? Less. Then is the cover greater or less than 25%? Greater. This worked well for species with high amounts of cover but was not useful for species with low coverage values. The best way to estimate species with low coverage values was to work up in an additive way. I would mentally try to bunch all of the individuals of a given species in to a section of the plot and then estimate the coverage. Since the area of the plot was 50 sq m, the area of a 4 dm (16 in) radius circle would be .5 sq m or 1% cover. A corner 2 m square would be 8%; a strip 1 m wide along one 5 m side would be 10% or 2 m wide would be 20%. These were the mental exercises that were the most useful to me. For the tree species, I recorded the cover in two categories: cover for trees with a diameter at breast height (dbh) greater than 1 dm and cover for trees less than 1 dm dbh.

There were many species that I did not know. However, I made collections of the unknowns and coded those collections to the species list so that later the name could be linked with the coverage and sociability indexes. As the other data sheets were completed for the releve, I continued to be alert for new species to add to the species list. Generally, these would be plants with trace amounts of cover, but the lowest cover value I recorded was 1%. The rationale was that if a species occurred on the releve then it would be weighted to at least 1% cover.

Peak Growth

A source of variation in this study occurred because of the time of the growing season when the sample was taken. My first releves were taken in early July and the last in late August. Thus some of the data were taken before peak growth and others after peak, in some cases late in the growing season. Species vary greatly in phenology; some develop early and others mature late in the season after the typical peak for most species. H. lanatum matures earlier than many other species. I used two techniques that helped to compensate for the difference in peak growth from area to area. For the most part, I selected releves at the lower elevations in each of the general locations early in the field season and then worked at the mid and higher elevations again in each area later in the field season. Also, later in the season I "reconstructed" cover for certain species including H. lanatum that were past peak and the foliage was drying and withering. I tried to visualize the plants of each species as if still healthy and fully developed and based the cover estimate on that cover reconstruction. I did not try to "project" cover to peak production at the beginning of the field season. The field work began in early July which approached peak production at the lower elevations.

New and Young Plants

The next step in data collection was to obtain information about individual new (seedling) and young (not sexually mature) H. lanatum plants and the micro site where they were growing. The seedlings were assumed to be current year's seedlings. They almost always had a single simple leaf and were usually less than 10 cm tall. Young plants had one or more simple or compound leaves but were notably larger than the seedlings, yet the plant showed no evidence of ever having a flowering stalk. To accomplish this I divided the releve into 4 quadrants numbered clockwise beginning at the top left corner. I followed a systematic way of looking for these two classes of individual H.

lanatum. I began at the corner range pole and worked along the diagonal to the center of the releve and sampled the first new and the first young H. lanatum encountered. I crawled on my hands and knees to the center and up to the top side of the plot or down to the baseline depending on the quadrant I was doing and then along the outside edge of the quadrant back to the corner pole and continued along the outer edge either down or up the outer edge to the midpoint of the side and then back to the center of the plot. If individuals were not found in that quadrant, then I went to the next quadrant. My goal was to collect 4 new and 4 young plants from each releve. Some times these plants were very easy to find and other times much more difficult. At times I could not find all 4 of each while other times I could not find any new or young individuals.

Once the individual was identified, a 10 cm radius plot frame was placed with the new or young plant in the middle of the plot. The percent surface coverage of litter, mineral soil, rock and moss/lichens was estimated and summed to 100%. Then the percent herbaceous and woody vegetation less than 50 cm was estimated for each. Also, the number of other new and young H. lanatum plants in the small plot was recorded, and I indicated the litter type and litter depth at the location where the plant was growing. These data would help me get a better understanding of the microsites where H. lanatum germinated and more importantly where the germinated seedlings could actually become established young plants developing eventually into mature plants.

After collecting those data for the individual plant, I excavated the plant and recorded the number and type of leaf (or leaves), length of the longest leaf, length of the taproot, rootcrown diameter, and if a seedling whether or not the cotyledons were present. All 8 of these new and young plants were bagged separately and brought back to Missoula to be dried and weighed. Any noteworthy details about this part of the data were also recorded.

This was a time-consuming part of the data collection. On some releves it was easy to find 4 individuals while others were much more difficult. In several cases, I could not find any of a certain maturity class of _H_. _lanatum_. But in retrospect this was an important part of the field work because it caused me to look very closely at a number of seedling and small plants and their related microsites. Without this close hands-on experience, I probably would have overlooked much of the detail about _H_. _lanatum_ that I gleaned from the study.

Soils Data

After all of the vegetation data were collected, I began to record data for several soils characteristics. Three samples of the surface 10 cm were collected and placed in plastic ziplock bags to be analyzed in the lab for percent organic matter. The 3 sample points were subjectively located near the center of the left half of the plot, near the center of the plot and near the center of the right half of the plot and numbered in that order. In addition, I dug a soil pit near the center of the plot at the same point where the second sample was collected for organic matter. (In certain cases such as in Glacier National Park, I did not dig the pit much beyond the 10 cm sample, but I completed the soils data by using a soils tube.) After the pit was dug, I measured the thickness of each horizon and collected a sample from that horizon to bring back to the lab for analysis of soil texture. If mottling was present in the soil profile, I measured the depth to mottling and recorded classes for abundance, size, and contrast. If gleying occurred, depth in the profile was also recorded. Parent material, rockiness, and HCL reaction were all record along with other subjective notes and comments about the soils.

Site Disturbance Factors

H. lanatum often grows in disturbed sites. Therefore, I recorded for each releve the intensity, frequency, and time since disturbance of 14 different disturbance factors: avalanche, flooding, thinning, seed tree cut, clear cut, clear cut/pile and burn, clear cut/broadcast burn, wildfire, road cut, road fill, rodent activity, wildlife use, livestock grazing, and windthrow.

Barriers to Usage

Barriers exist some times that deter animals from readily foraging on *H. lanatum*. I recorded the distance, if any, from the releve to each of 8 different barriers: roads, steep slopes, talus, cliffs, large rocks, slash piles, plants, and water. Any other observations about the barriers or disturbance factors were also recorded.

Lab Methods

Species Identification

I spent a considerable amount of time working on the identification of the voucher specimens and unknowns collected on the releves. Peter F. Stickney graciously provided the verification or the identification for many of the specimens. A complete species list was prepared and the correct species names were added to the field data sheets for Canopy Coverage.

Elevations

I did not feel comfortable with some of the variation in elevations obtained from the altimeter carried in the field. Therefore, all of the elevations for these releves were read directly from the 7.5 min topographic maps at the Mansfield Library. From the marks and notes that I made on the field maps, I located fairly quickly and accurately where the plots were and what the correct elevation was. A set of orthophotoquads was also available at the library's map room. I could actually detect local features in the photos that confirmed the plot was pinpointed correctly of the map.

Dry Weights

During the field season 112 new and 127 young *H. lanatum* plants were randomly collected. Each plant was placed in a separate paper bag, air dried and stored at the lab. Later, I oven dried the samples for at least 24 hrs at 70 degrees C, then removed the plant from the bag, separated the root from the stem and weighed both parts of the plant.

If the weight was less than 0.5 g, I used the analytical balance; otherwise, the plants were weighed on a top loading digital balance. New plants were weighed to the nearest 0.001 g and young plants to the nearest 0.01 g.

Soil Textures

Originally my plan was to texture the soils by feel in the field. I had obtained several standard soil samples with known percentages of sand, silt and clay. However, I was not entirely comfortable with my experience to texture soils so I also collected a sample from each horizon in the profile. After a few releves, attempts to texture the soils in the field were dropped, and samples were collected for later analysis. Organic soils or mineral soils high in organic matter are more difficult to texture, especially by feel, because the organic matter present tends to mask the true texture. Many of the soils collected from these releves were high in organic matter which made the determination of texture for those soils difficult.

A contract was arranged with Mr. Arial (Andy) Anderson, retired soil specialist formerly with the Soil Conservation Service, to texture the soils collected from the releves. His years of experience with the soils of western Montana proved a great help. The standard soil texture triangle has 12 different classes. The soils from the releves belonged to 8 of the 12 classes but none of the soils had more than 40% clay or 80% silt. He further subdivided the mineral soils into 15 classes; a 16th class was organic soils.

Percent Organic Matter

Three soil samples of the surface 10 cm were collected at each releve. At the lab each sample was sieved through a 1.981 mm mesh soil tray to exclude any particles of gravel or organic matter larger than 2 mm. Several small scoops of soil (about 5-10 g total) were taken randomly from different parts of the soil tray and placed in a ceramic crucible of known weight. Because of the space limitations in the desiccator and muffle furnace and the time it took to prepare the samples, 30 samples were the most I could process at one time. The samples were placed in a drying oven for 24 hrs at 105 degrees C. This dried the samples completely. I removed the samples from the drying oven and placed them in a desiccator for 30 minutes to cool before weighing on a top-loading digital balance. After recording the dry weights, I placed the crucibles in the muffle furnace for 4 hrs at 550 degrees C. Following that treatment which ashed all of the organic matter, the samples cooled for 30 minutes in a desiccator, and then each sample was reweighed to get the ashed weight. The percent organic matter was the net ashed weight divided by the net dry weight and multiplied by 100 and subtracted from 100.

I ran 4 batches of 30 samples each, 1 batch of 27 samples and a final batch of 20 samples. During the final batch I repeated 4 samples that spilled previously and made a 10% double check with duplicates of 16 samples.

VEGETATION DATA ANALYSIS

Cover Data and Table Work

Data were initially analyzed utilizing an association table (Mueller-Dombois and Ellenberg 1974). The association table lists all species in the study (rows) by all releves in the study (columns). Releves may then be combined and the constancy (frequency of occurrence) and the mean coverage (based on the releves where the species occurred) can be calculated. Both the association and constancy/coverage tables may be simplified if the number of species is reduced and/or releves are combined together into subgroups. The table provided initial indications of which species occurred most frequently and in greatest abundance, particularly in certain subgroups of releves. Also, where possible the releves were keyed to forest habitat type (Pfister et al. 1977), riparian habitat type or community type (Boggs et al. 1990).

First, I created a data file with numeric species codes and cover values for all species in all releves. Data were double-checked and a synthesis (or association) table generated which listed all of the species in the study alphabetically (rows) by all of the releves in the study (columns). Next, a constancy/coverage table was generated which again listed each species in the dataset with its corresponding constancy (percentage of occurence in the releves) and coverage (averaged from the releves where the species occurred). The file of double-checked data for species coverages on each releve supplied the FUZPHY program data to generate an association table of all species by all releves. From the same data, the program also generated a constancy/coverage table. The association tables and constancy coverage tables provided the opportunity to scan the data and look for trends and relationships.

Next, I used a number of multivariate methods to analyze community data. There are at least three general schools of thought about ways to understand the relationships that occur in multivariate community data: direct gradient analysis, ordination and classification. Gauch (1982) described the merits of using a combination of all three methods to unravel and explain complex environmental interactions that exist in many plant communities. These are not statistical techniques but rather yield output suited to pattern analysis. To identify and explain the various patterns that occur in the data becomes the challenge and goal of analysis and interpretation. I used specific techniques from all three general approaches to analyze these 49 releves.

Data analysis may be described in stepwise or chain-reaction fashion, but in reality the process did not cascade smoothly without interruption. A brief summary of each analytical approach follows. This is not necessarily given in the same sequence the data were analyzed, nor is the order prioritized by perceived importance of the results. However, this overview establishes the foundation for the discussion which follows this chapter. This is how I analyzed the data to understand the environmental requirements of Heracleum lanatum, explored the hypotheses presented in the initial study plan, and met the study's 2 objectives.

Models and Gradients

In order to better understand subsets of releves that had similar attributes in common, I developed two models and two gradients which were applied to all of the releves in the study. The code, description and number of releves in each class of each model or gradient is shown in Table 2.

The riparian model (RIPARMOD) separated avalanche, streamside and other riparian from those releves not considered to be riparian in that water in excess of annual precipitation was not available on the site. The 49 samples were divided into 4 classes depending on the site's riparian nature.

A cover model (COVERMOD) was also constructed by dividing the 49 releves into 6 classes depending on the type of overstory cover. These classes were conifer cover greater than or equal to 25%, conifer cut (clearcut), conifer mesic microsite openings (0-20% conifer cover, but with conifers surrounding), hardwood tree cover greater than or equal to 25%, tall shrub cover greater than or equal to 25%, and other samples without overstory cover.

About the time I was pondering the possible environmental gradients, I began to think in terms of abundance gradients. This was a study to examine stands with a full range of abundance of mature *H. lanatum*. I set up a 5-class abundance gradient for mature *H. lanatum* based on the estimated cover from each releve as follows: 1) cover class 1 equals 1-5% *H. lanatum* cover, 2) cover class 2 equals 6-9%, 3) cover class 3 equals 10-17%, 4) cover class 4 equals 18-45% and 5) cover class 5 equals 46-90%.

Table 2. Two models and two gradients used for the analysis.

Overstory Cover Model (COVERMOD)

Code	Description	(n)
1	Conifer cover >/= 25%	8
2	Conifer cut (clearcut)	3
3	Conifer mesic microsite openings (0-20% conifer with conifer surrounding)	6
4	Hardwood tree cover >/= 25%	2
5	Tall shrubs >/= 25%	10
6	NA	20

Riparian Model (RIPARMOD)

Code	Description	(n)
1	Avalanche	16
2	Streamside	15
3	Other riparian (not stream side)	8
4	NA	10

Cover Gradient for Mature *H. lanatum* (HELACOVC)

Code	Description		(n)
1	HERLAN cover	1 - 5%	10
2	HERLAN cover	6 - 9%	9
3	HERLAN cover	10 - 17%	9
4	HERLAN cover	18 - 45%	13
5	HERLAN cover	46 - 90%	8

Gradient for New-Young-Mature Abundance Cube (NYMABUNC)

Code	Description			(n)
	New	Young	Mature	
1	Low	Low	Low	8
2	High	Low	Low	4
3	Either	High	Low	16
4	Either	Low	High	12
5	Low	High	High	3
6	High	High	High	6

However, it occurred to me during the data analysis that in addition to describing sites that had high coverages of *H. lanatum*, I also should be interested in identifying and understanding those areas which had high densities of *H. lanatum* seedlings and young plants. Such densities were not counted in the field, so I devised a way to estimate these densities indirectly.

When the data were collected for new and young *H. lanatum*, sometimes I found the 4 sample individuals of each quickly but other times it was much more difficult. At times, no new or young were found. Based on this information, I constructed two gradients: one for new and one for young *H. lanatum*. There were 9 abundance classes initially, but later I combined some classes so that each gradient for new and young had only 5 classes (Table 3).

Table 3. New and young reproduction initial abundance classes and combined abundance classes.

	Initial Abundance Class	Combined Abundance Class
Presence described as abundant	9	5
One from each quadrant and some additional (or other comments of being plentiful)	8	5
One from each quadrant	7	4
All collected but not from all quadrants	6	4
One missing but time was a factor	5	3
One missing	4	2
Two missing	3	2
Three missing	2	1
All four missing	1	1

The final gradient, New-Young-Mature Abundance Cube (NYMABUNC), is constructed from the first 3 gradients directly. I use the term gradient; the abundance cube is conceptually, but not exactly, linear. The abundance cube is divided into 6 cells described with the following algorithum:

NYMABUNC 1 - New LE 2 and Young LE 2 and Mature LE 3

NYMABUNC 2 - New GE 3 and Young LE 2 and Mature LE 3

NYMABUNC 3 - Young GE 3 and Mature LE 3

NYMABUNC 4 - Young LE 3 and Mature GE 4

NYMABUNC 5 - New LE 3 and Young GE 4 and Mature GE 4

NYMABUNC 6 - New GE 4 and Young GE 4 and Mature GE 4

The volume of space defined contains all 49 releves and is illustrated in Fig. 3. This conceptual model should be applicable to most plant species and may be a key insight derived from this study.

The name, general location and group for the 2 models and 2 gradients are shown for each releve in Table 4.

Direct Gradient Analysis

I used direct gradient analysis to explore influence of various environmental parameters on the abundance of *H. lanatum*. Percent canopy coverage is one indicator of abundance. Other descriptors of abundance were the new, young and mature categories, the two-way combined categories of those 3 classes, and the 6 cells of the NYM abundance cube. Specific environmental factors that I compared by direct gradient analysis were slope, aspect, elevation, configuration, topography, organic matter, and soil texture. These factors were correlated with

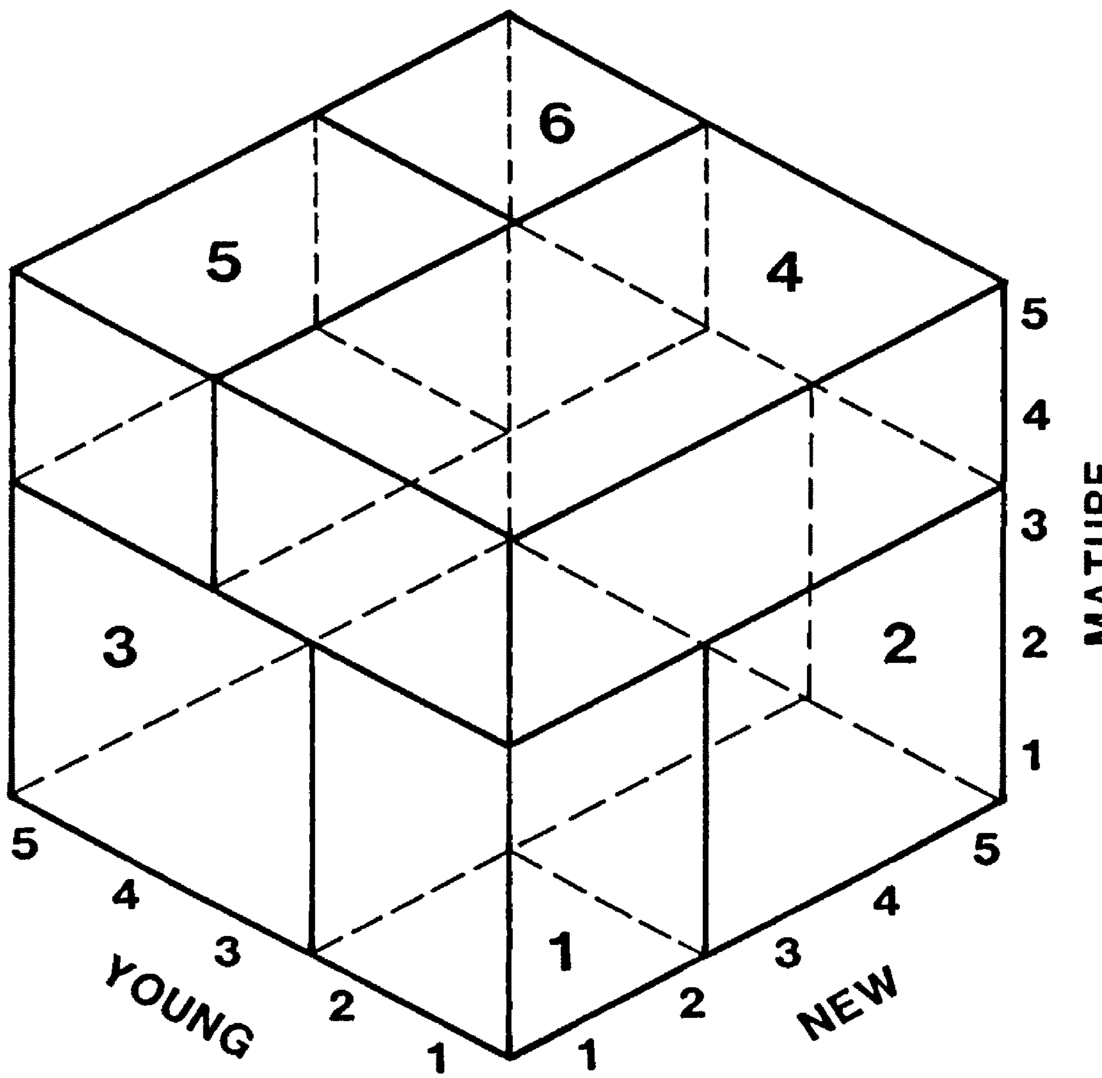

Fig. 3. Conceptual illustration of the new-young-mature abundance cube which integrates the abundance of all 3 categories into a single gradient with 6 cells.

Table 4. Releves by models and gradients and forest or park.

Releve	Releve Name	F/P	COVERMOD	RIPARMOD	HELACOVC	NYMABUNC
1	Lolo Cr POFO	LNF	NA	Streamside	4	4
2	Howard Cr	LNF	Tall Shrubs	Streamside	5	6
3	Lost Cr THPL	FNF	Conifer	Streamside	1	3
4	McGee Cr	GNP	Tall Shrubs	Streamside	4	6
5	Camas Rdg Open	GNP	NA	NA	2	1
6	Camas Rdg ALIN	GNP	Tall Shrubs	Other Riparian	4	4
7	Camas Rdg Seep	GNP	Conifer Opening	Other Riparian	5	4
8	Camas Rdg PIEN	GNP	Conifer	NA	2	2
9	Dutch Cr	GNP	NA	Other Riparian	4	4
10	Anaconda Cr	GNP	NA	Streamside	5	4
11	Lone Pine POTRE	GNP	Hardwood Trees	NA	5	6
12	Lost Cr PTAQ	FNF	NA	Avalanche	4	4
13	Ft Fizzle PIPO	LNF	Conifer Opening	Streamside	4	6
14	Ft Fizzle Open	LNF	Conifer Opening	NA	1	3
15	Ross Cr	KNF	Conifer Opening	NA	4	4
16	Bear Cr Meadow	KNF	NA	Avalanche	2	3
17	Bear Cr SARA	KNF	Tall Shrubs	NA	5	5
18	Loon Lk Conifer	KNF	Conifer Opening	Other Riparian	2	3
19	Loon Lk ALIN	KNF	Tall Shrubs	Streamside	5	6
20	Bear Cr ACGL	KNF	Tall Shrubs	Avalanche	3	3
21	Bear Cr PIEN	KNF	Conifer	Other Riparian	1	1
22	Bear Cr Nfacing	KNF	NA	Avalanche	1	1
23	Bear Cr Sfacing	KNF	NA	Avalanche	2	3
24	Griffin Cr Con	FNF	Conifer	Streamside	1	3
25	Griffin Cr Bog	FNF	Tall Shrubs	Streamside	3	3
26	Lost Cr ACGL	FNF	Tall Shrubs	Avalanche	3	1
27	Avalanche RUPA	GNP	NA	Avalanche	2	3
28	Avalanche POTRI	GNP	Hardwood Trees	Streamside	4	5
29	Logan Cr THOC	GNP	NA	Avalanche	4	4
30	Logan Cr RUPA	GNP	NA	Avalanche	4	5
31	Hay Cr OSOC	FNF	NA	Avalanche	3	3
32	Hay Cr RHAM	FNF	Tall Shrubs	Avalanche	3	2
33	Packers Rt ABLA	GNP	Conifer	Streamside	2	1
34	Packers Rt SYAL	GNP	NA	Avalanche	1	1
35	Hay Cr EPAN	FNF	Conifer Cut	NA	3	3
36	Hay Cr Dry	FNF	Conifer Cut	NA	2	3
37	Lolo Pass OSOC	LNF	Conifer Opening	Other Riparian	1	2
38	Lolo Cr Rock	LNF	NA	Streamside	5	6
39	Bull Lake	KNF	NA	Streamside	4	4
40	Lolo Cr Ski Tr	LNF	NA	Streamside	3	2
41	Lolo Cr RHAM	LNF	Tall Shrubs	Streamside	2	3
42	Lost Johnny Cr1	FNF	NA	Avalanche	3	1
43	Lost Johnny Cr2	FNF	NA	Avalanche	5	4
44	Granite Cr ABLA	FNF	Conifer	NA	1	1
45	Granite Cr Open	FNF	Conifer Cut	NA	1	3
46	Granite Cr PICO	FNF	Conifer	Other Riparian	1	3
47	Marias Pass	FNF	Conifer	Other Riparian	3	3
48	Lost Johnny Cr3	FNF	NA	Avalanche	4	4
49	Lost Johnny Cr4	FNF	NA	Avalanche	4	4

the models and gradients explained above and the biomass data for new and young species. In the study plan, I had proposed 5 curves as various hypotheses I originally held about how _H. lanatum_ responded to certain environmental factors (Fig. 4).

I characterized the site descriptors, environmental data (including soil texture and organic matter), and biomass data for _H. lanatum_ reproduction by using a combination or one or more descriptive statistics: frequency, mean, standard deviation, minimum, maximum and range.

Ordination

The ordination technique applied to these data was Detrended Correspondence Analysis (DCA or DECORANA). From Gauch (1982), I determined DCA would be the ordinational method of choice for the type of species data from these 49 releves. DCA is a refinement of reciprocal averaging (RA) that corrects for two major disadvantages of RA: the arch effect and concentration of samples at both ends of the gradient. The RA technique is conceptually similar to weighted averages, but the computation resembles an eigenanalysis problem akin to principal components analysis. As in RA, DCA ordinates species and samples simultaneously. Documentation for DCA is found in Hill (1979a). I accessed the program through the FUZPHY package (Roberts 1989) on the VAX system at the University of Montana.

A major step in the data analysis was to complete an ordination with DCA of the species cover data for all species in all releves. The output contained lists of coordinates for 4 axes to locate each of the

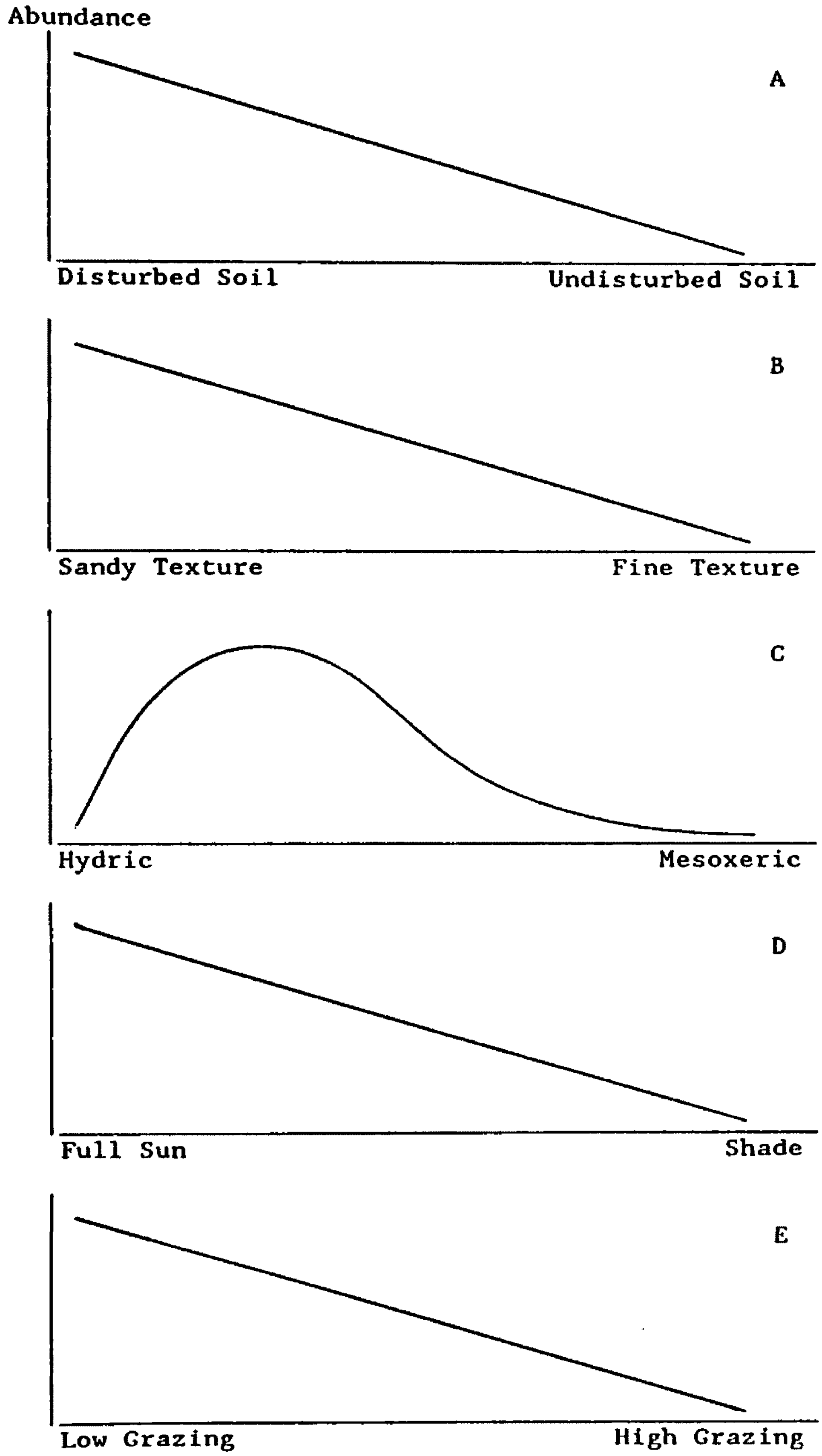

Fig. 4. Initial hypotheses--possible responses of *H. lanatum* abundance to 5 different environmental gradients.

releves and each of the species in hyperspace. But I limited the data analysis and ordination construction to 3-dimensional space with the first 3 axes for both the releves and species. The plot procedure in SAS was used to arrange the 49 releves in space based on the values for the three axes. Much of later data analysis was based on "overlays" of this initial ordination of the releves. Next, I sought to identify environmental factors or other parameters that would fit the gradients formed by the 3 axes in this ordination. The releves did segregate somewhat into different "clouds" in the space which seemed to have relation to general cover types or landforms. Later subsets of the 49 releves were analyzed. Also, species with constancies greater than or equal to 25% were plotted in 3-dimensional space.

Classification

Various methods of classification are available; I chose to use Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979b) which seemed to be the classification method of choice for these data (Gauch 1982). This method is a polythetic divisive classification because values for all of the species in the data set are used in the computations, and the analysis begins with all species and samples and systematically divides the data into smaller and smaller groups that have individuals with greater and greater similarities, a hierarchical approach. I accessed TWINSPAN on the Forest Service's Data General system through the ECOPAC software developed in Region 1 (USDA Forest Service 1987).

Inductive Reasoning

Most of the results and conclusions that follow are based on information gleaned from the 49 releves in this study. Much effort was made to extract information that might apply to a majority of the *H. lanatum* sites that may occur in the area of this study. However, the fact remains that the results which will be discussed pertain to the samples taken in this study.

Frustrations with the Data Analysis

It would be an oversight if I did not refer to the frustrations experienced while attempting to analyze these data. I found comforting expressions in several chapters by Gauch (1982). One paragraph seems especially appropriate: "The reality (is) that community ecologists study has been characterized by Whittaker (1952:31) as 'loosely ordered, complexly patterned, multiply determined.' An ecologist need not apologize for 'the difficulty of his field, the necessary limitations of his data, statistical involvements of his work, partial indeterminacy of his results, and the slowness and laboriousness of progress.' Computer analyses using multivariate techniques are important tools for extricating useful results from complex community data."

RESULTS AND DISCUSSION

Gauch (1982) suggested the appropriateness of the presentation and interpretation of the results being discussed together in studies of this nature. Thus, I will blend the discussion with the results rather than present each separately. The conclusions drawn from this study are first stated, by objective, then the results and discussion are presented which led to these conclusions.

This study's first objective was to identify the probable environmental factors which influence the occurrence and abundance of *Heracleum lanatum*, particularly in areas where this species is abundant. I conclude that *H. lanatum* grows most abundantly in microsites (often areas of only 50 to 500 sq m though some sites may be substantially larger) that are depositionally disturbed, receive water in excess of annual precipitation and have undulating floodplains with slopes <5% adjacent to streams. *H. lanatum* can thrive in shade or full sun as long as the canopy cover is broadleaf. This species does not grow well under conifer canopies.

The second objective of this study was to identify plants (ecological equivalents) commonly associated with *H. lanatum*. The 7 species that were closely associated with *H. lanatum* in both TWINSPAN and DECORANA analyses were the following: *Alnus incana*, *Calamagrostis canadensis*, *Carex bebbii*, *Elymus glauca*, *Geum macrophyllum*, *Rubus idaeus* and *Urtica dioica*. The TWINSPAN analysis was for a reduced list of 48 species (and *Carex bebbii*). The DECORANA analysis was for the list of 38 species with constancy >/= 25%; *Alnus incana*, at 20% constancy, was an exception.

Environmental Factors

Existing Classifications

H. lanatum is an atypical species that does not fit neatly into the existing classifications. Twelve of the 49 releves keyed out to 8 different forest habitat types (Pfister et al. 1977) (Table 5). When the riparian and wetlands classification was used (Boggs et al. 1990), 9 releves keyed to a total of 6 different habitat types while another 12 went to 6 different riparian community types. Four releves fit both a riparian and a forest habitat type. However, in each case the riparian classification was a better fit. Of the 20 releves that did not fit any classification, all were disturbed sites: 14 in avalanche runout zones, 2 in clearcuts, 1 on a road fill and 3 in unclassified streamside types in widespread locations (Lolo Creek, Bull Lake on the Kootenai National Forest and Dutch Creek in Glacier National Park). It is understandable that these types of sites would not fit well in the classifications since avalanche chutes, clearcuts and road fills were excluded from areas sampled because of disturbance.

This species may be present in a wide variety of types, particularly in moist, depositionally disturbed locations. Other types may provide suitable habitat in areas outside the geographic boundaries of this study. However, only 4 (ABLA/CLUN/ARNU, ABLA/CLUN/CLUN, Picea/EQAR and TSHE/CLUN/ARNU) of the 8 forest habitats types and phases were a part of the 17 forest habitat types and phases which had stands with *H. lanatum* present in the classification of Pfister et al. (1977). For the riparian habitat and community types only 1 (*Alnus incana* c.t.) of the 12 was in the group of 5 where *H. lanatum* was mentioned

Table 5. Correlation of 49 releves with habitat types (h.t.) and community types (c.t.) in exiting classifications.

Releve	None	Forest h.t.	Riparian h.t.	Riparian c.t.
1	NA			
2				ALNINC
3		THPL/CLUN/ARNU	THUPLI/GYMDRY	
4				ALNINC
5		ABLI/CLUN/ARNU		
6				ALNINC
7				SYMOCC (?)
8		Picea/CLUN/CLUN		
9	NA			
10				SYMOCC (?)
11				POPTRE/POAPRA (?)
12	NA			
13			PINPON/CORSTO	
14				SYMOCC (?)
15				CORSTO (?)
16	NA			
17	NA			
18		TSHE/CLUN/ARNU		
19				ALNINC
20	NA			
21		TSHE/CLUN/ARNU		
22	NA			
23	NA			
24		Picea/EQAR	ABILAS/CALCAN/CALCAN	
25		Picea/EQAR	Picea/EQUARV	
26	NA			
27	NA			
28				POPTRI/POAPRA
29	NA			
30	NA			
31	NA			
32	NA			
33		ABLA/CLUN/ARNU	ABILAS/STRAMP/LIGCAN	
34	NA			
35	NA			
36	NA			
37			ABILAS/STRAMP/LIGCAN	
38				SPIDOU
39	NA			
40				SPIDOU
41			ABILAS/CALCAN/CALCAN	
42	NA			
43			CALCAN	
44		ABLA/ARCO		
45		ABLA/ARCO		
46		ABLA/CLUN/CLUN		
47		ABLA/CAGE/CAGE		
48	NA			
49			CALCAN	

Table 5. Continued.

Forest Habitat Types

Abies lasiocarpa/Arnica cordifolia h.t.
Abies lasiocarpa/Carex geyeri h.t.
  Carex geyeri phase
Abies lasiocarpa/Clintonia uniflora h.t.
  Aralia nudicaulis phase
  Clintonia uniflora phase
Picea/Clintonia uniflora h.t.
  Clintonia uniflora phase
Picea/Equisetum arvense h.t.
Thuja plicata/Clintonia uniflora h.t.
  Aralia nudicaulis phase
Tsuga heterophylla/Clintonia uniflora h.t.
  Aralia nudicaulis phase

Riparian Habitat Types

Abies lasiocarpa/Calamgrostis canadensis h.t.
  Calamagrostis canadensis phase
Abies lasiocarpa/Streptopus amplexifolius h.t.
  Ligusticum canbyi phase
Calamagrostis canadensis h.t.
Picea/Equisetum arvense h.t.
Pinus ponderosa/Cornus stolonifera h.t.
Thuja plicata/Gymnocarpium dryopteris h.t.

Riparian Community Types

Alnus incana c.t.
Cornus stolonifera c.t. (?)
Populus tremuloides/Poa pratensis c.t. (?)
Populus trichocarpa/Poa pratensis c.t.
Spiraea douglasii c.t.
Symphoricarpos occidentalis c.t. (?)

? = considered opinion, but with some reservations specifically in the text or tables as common for that type. Although *H. lanatum* had been documented in numerous types it did not show a strong affinity to any one type in those studies. Also, many of the types of sites and conditions that seemed to favor this species were logically excluded by definition from even being sampled because of the disturbed, microsite, and/or atypical nature of the sites. When the releves were selected for this study, sites with very high abundances of *H. lanatum* were sampled. Hopefully, these samples included many, if not most, of the conditions where *H. lanatum* thrives within the study area. However, these classifications reported *H. lanatum* present in at least 13 forest habitat types and 4 riparian types not represented by these 49 releves.

A pattern for *H. lanatum* to grow abundantly in disturbed areas is suggested by the mean cover of *H. lanatum* for the 4 groups in Table 5. Mean cover in various types was as follows: the unclassified group had 19.0% (s=15.1, n=20), forest habitat types had 7.2% (s=4.0, n=12), riparian habitat types had 19.0% (s=23.1, n=9), and riparian community types had 44.3% (s=28.4, n=12). Although the standard deviations were large, the inference is made that *H. lanatum* grows quite abundantly in sites keyed to riparian community types. The community types generally represent the more disturbed types of sites included in the classification which do not support climax vegetation.

I also assessed how these types correlated with the abundance gradient NYMABUNC. None of the releves in classes 4, 5 or 6 showed affinity to a certain group, nor did any key to a forest habitat type. Releve 13 (NYMABUNC=6) was the only sample to key to a conifer type in the riparian classification. In these 49 releves, *H. lanatum* does not grow abundantly under conifer canopies.

The *Alnus incana* c.t. was represented by 4 releves (the greatest number of samples to key to a single type) with percent cover values for *H. lanatum* of 90, 70, 40 and 25 ($\bar{x}$=56.3). Three of these releves, with the mean *H. lanatum* cover of 61.7%, comprise half of the releves in NYMABUNC-6. Clearly, the *Alnus incana* c.t. is a type that can provide extremely favorable conditions for the abundance of new, young and mature *H. lanatum*. However, other types were also capable of producing abundant populations of *H. lanatum* as well as other sites (e.g., avalanche chutes) not represented in the existing classifications.

Microsites

The rationale used to suggest that *H. lanatum* grows most abundantly in microsites is two-fold. Cover for *H. lanatum* in the releves in this study was substantially greater than for the other classification studies conducted in northwestern Montana. For the Forest Habitat Types of Montana, *H. lanatum* occurred on 20 stands for the 3 national forests in northwestern Montana. Of the 20 stands, *H. lanatum* cover was a trace (0.5%) on 13 and present (3%) on the remaining 7 stands. Boggs et al. (1990) reported *H. lanatum* in stands up to 25% cover, but 14 (more than one fourth) of my releves had *H. lanatum* cover greater than or equal to 30%. I suggest the main reason this happened is because *H. lanatum* often occurs in microsites. The kinds of microsites that would have been logically excluded from the samples taken for these classifications because these microsites are atypical of the surrounding vegetation and are often quite small. However, these are often the kinds of sites best suited for H. lanatum.

Sites where H. lanatum grows abundantly and exceeds 25% cover were excluded from all of the habitat or community type classifications done for Montana. This exclusion occurred for one or two reasons. H. lanatum occurred in a microsite that was considered atypical for the overall stand and/or the site was disturbed, e.g., avalanche chute runout zones.

Mean stand size was a confirmation of this microsite concept. Results of the estimates of stand size for the area occupied by H. lanatum ranged from 0.05 to 5.0 a with a mean of only 0.59 a. Stand size was not deemed a determining factor in predicting the abundance of H. lanatum for the two models and two gradients analyzed.

Riparian Areas

A single feature provides a broad definition of a riparian area: water available for plant growth occurs in excess of the amount of precipitation received on that site during the year. Such areas include streamside sites that may be flooded during parts of the year (usually spring or early summer) and/or allow the possibility of subirrigation to vegetation growing near the stream. Other kinds of riparian areas are toe slopes of avalanche chutes, perched water tables and other types of seep areas. Again, with inductive reasoning and pattern analysis of the subjective data recorded about riparian characteristics, it became apparent that abundant H. lanatum was often associated with riparian areas. I caution that not all riparian areas are suited for this species. For example, riparian areas with abundant conifer overstory would not be well suited for _H. lanatum_.

Depositional Disturbance

As the analysis progressed, it became apparent that many of the releves with abundant _H. lanatum_ were disturbed sites. Data collection included a subjective evaluation of apparent or possible types of disturbance. By inductively considering various types of disturbances, I came to realize that much of the disturbance that appears to favor abundant _H. lanatum_ is depositional in nature. Four types of depositional disturbance are riparian floodplains, runout zones at the toe slope of avalanche chutes, fill slopes on road cuts, and rodent (primarily pocket gopher) activity. Releves with abundant _H. lanatum_ often had one or more of these types of disturbance associated with that site.

At least four types of depositional disturbance provide good sites for _H. lanatum_. Two are major factors and two less significant. Alluvial banks of streams and runout zones at the bottom of avalanche chutes are important types of disturbance. Of less importance are the fill slopes of road cuts and moist meadows with abundant rodent activity. Depositional disturbance benefits _H. lanatum_ in at least two ways. First, since the disturbance is accumulative, the roots of the plant are not displaced or exposed (as would occur with erosive action) and the plant is prepared with ample carbohydrate reserves to push up through the newly added soil. At the same time the disturbance reduces competition from other species that must seed in and become established;

H. lanatum is already established and growing. Fill slopes may be an exception in that H. lanatum must also become established as well when the cut is new. In certain areas the fill slope may also accumulate new material each year from soil or gravel being washed or plowed from the adjacent road surface.

Configuration, Topography and Slope

A unique combination of these three environmental factors was commonly associated with releves having abundant H. lanatum. The combination which supports the most abundant stands is that of undulating stream bottoms with slopes less than 5%. This pattern is readily seen in Table 6 where the combination occurs in 10 releves. Included are five of the six releves in NYMABUNC Cell-6. Five other releves share this pattern but do not have abundant H. lanatum for a number of reasons. Releves 3 and 24 had a conifer canopy, and releves 1, 10 and 39 had low abundance values for young H. lanatum although the coverage values for mature H. lanatum were high.

TWINSPAN

This analytical method provided an excellent way to visualize the important features of the data on a single page. TWINSPAN was possibly the most helpful technique to illustrate certain patterns. Fig. 5 shows the results with a column for each of the 49 releves and rows for the 48 species objectively deemed the most important by the program. This classification simultaneously works with both samples and species. The columns for those releves considered most similar are arranged close

Table 6. Characteristics of releves within the 6 new-young-mature abundance classes.

Releve	Topograp 1/	Config 2/	Slope (%)	Elevation (ft)	Aspect	Stand Size (a)	HERLAN Cover (%)
NYMABUNC-1							
5	1	2	10	3870	70	1.00	7
21	4	3	14	3970	190	0.05	5
22	4	2	33	3990	315	0.25	5
26	4	2	22	4760	130	0.15	10
33	5	4	9	3650	180	0.35	7
34	3	4	17	3690	245	0.05	2
42	4	2	24	4780	45	0.35	10
44	4	4	15	5010	285	0.10	1
NYMABUNC-2							
8	4	3	25	3870	180	0.05	8
32	4	4	30	5330	105	0.50	15
37	4	2	56	5100	270	0.75	5
40	6	4	2	4190	290	0.35	10
NYMABUNC-3							
3	6	4	3	3660	320	0.05	5
14	6	2	1	3320	85	0.10	2
16	4	2	15	4030	105	2.50	8
18	4	3	22	3610	40	0.05	8
20	4	4	42	4060	120	0.35	10
23	4	2	24	4000	145	0.25	8
24	6	4	4	4660	160	0.15	3
25	6	4	5	4610	195	0.75	15
27	3	1	45	3680	215	1.00	6
31	4	2	29	5280	130	1.50	15
35	5	4	7	4300	150	0.15	10
36	4	4	12	4580	145	1.50	6
41	6	2	2	4200	315	0.20	6
45	4	4	12	5020	295	0.05	3
46	5	4	3	5020	145	0.75	4
47	5	2	3	5240	285	0.75	10
NYMABUNC-4							
1	6	4	3	4300	50	0.35	25
6	4	3	15	3870	190	0.50	40
7	4	3	13	3870	185	0.05	60
9	6	4	3	3650	190	0.25	20
10	6	4	1	3590	155	0.35	60
12	4	2	15	4760	225	1.00	40
15	5	4	8	2830	100	0.25	20
29	2	1	40	5600	170	0.50	25
39	6	4	1	2340	355	0.20	35
43	5	2	14	4790	60	0.75	75
48	3	4	42	5200	70	0.10	40
49	4	3	20	4800	60	5.00	25
NYMABUNC-5							
17	4	4	13	3980	195	0.10	60
28	6	4	5	3460	185	1.50	25
30	3	2	28	5640	255	0.75	30
NYMABUNC-6							
2	6	4	2	3940	130	0.20	90
4	6	4	4	3720	300	0.05	25
11	5	2	3	3580	150	1.50	80
13	6	4	2	3320	120	0.05	30
19	6	4	3	3600	90	0.75	70
38	6	4	2	4220	355	0.75	50

1/ Topography: 1=ridge, 2=upper slope, 3=mid slope, 4=lower slope, 5=bench or flat, and 6=stream bottom

2/ Configuration: 1=convex, 2=straight, 3=concave, and 4=undulating

RIPARMOD	3 3	223	33	1112	3321	1111	1 1	1111	2 32	22	2112	22222	Avalanche
COVERMOD	2111	111	1335	55 1	5345		22		33	43 5	5 5	5 5	Conifer, Tall S.
HELACOVC	1311	1112	2215	3342	4543	2244	3323	4211	4145	5445	5544	34532	Low End
NYMABUNC	3313	3311	2325	3141	4452	2345	3331	4311	6344	6446	6446	34623	NYM = 6

```
                    44442 2  1312243  231223333412321 1113 144 2 344
                    5746431588770683678263901562274234901592939451801

 141 PIC  ENG       11748161911-1---12---------1-----------------15----   000001
  27 ARN  LAT       -5-54----6---------------1----------------1----------   000010
  43 BRO  VUL       1212212--71-1-21--1------2-1-------------1------   000010
  66 CLI  UNI       ----114262----11-1--------------2-----------------   000010
  95 FRA  VIR       9221---221--------1-----------1---1-------1-------   000010
   2 ABI  LAS       --721--1121--1-8----------1-------------------1   000011
 106 GYM  DRY       ----1481-------18--1------------------------1-----   000011
   6 ACT  RUB       --11211112--21-2-11--11-1--1----1----------1-----   000100
 210 TIA  UNI       ----226--622--26--1-------------------1-----------   000100
  76 DIS  HOO       -----12121-117--221---11----11-------1------------   000110
   3 ACE  GLA       -----1------89----1-------------------1-----------   001010
 186 SAM  RAC       ------1---27222---1412--22111--1----------2-------   001010
  41 BRO  CAR       --------------------1-1455-8-2-2------------6------   001100
  81 EPI  ANG       221----11--21-2----4171999698211--12-----51---1-1   001100
  60 CIR  ALP       -----1----42--141111-------1-------1------2-------   001101
 179 RUB  PAR       1-42-148566428755-1--78-624477-------5--1111---   001101
 222 VER  VIR       ------11131-11-11-2-1--22--12--7--------1-2-------   001101
 227 VIO  CAN       -11----65262252-66452-2221-284222---12--5116-----   001101
 133 OSM  CHI       -111111121-1-2-1226-----6--------22-1-2-------------   001110
  30 AST  FOL       111-1112-1--------11-11212---34-1---1-------11--1-   001111
 208 THA  OCC       16562144211622112215128-21111115-122--1--124---2   001111
 190 SEN  PSE       252112-41--------44-------------------7-4----------1-   010010
  35 ATH  FIL       ----1-7----211221-1------1-5----6----2-12---1-1--   010100
 194 SMI  STE       ----11-122-12--112111----2--212-1-22221----1--11-   010101
 204 SYM  ALB       ------2256---1-628---4---1--879-8829811----1-----   010101
 205 TAR  OFF       1-1-11-1----1----1-------111-11-12211-1--1-1-----   010101
  93 FES  SUB       ------11-24222-451151-1121-1---2112--5127-----1-1   01011
  98 GAL  TRI       ---11222424-2242555111222-21221142264-71142--11   01011
 170 RHA  ALN       ----------------6--9---------------------------------9   01100
  49 CAR  DEW       -----------8411-1-1------8-2-1--21-----1-42-------   011011
 131 MON  SID       -----------52--5-------1-------2-----6--2----------   011011
  80 ELY  GLA       221-21-661-21---24--99212521122---44482-56521--22   1000
  18 ANG  ARG       111-11-411------12--1-1-1-1--2----11211-12-21--11   10010
 160 PTE  AQU       -------------14-------1------8528-----99----5------   101001
  59 CIN  LAT       -----2------21---225------1-4---------11--622-----2   101011
 218 URT  DIO       -----1------725221-22121222-27221--24241462 1--1--1   101011
 178 RUB  IDA       ----11-------1-2-1-----21-125-21211-2-12-1-22--511   101100
 109 HER  LAN       2412222333284473786533675424721271689679996656842   101101
  84 EQU  ARV       ---141--1------21-4------1------2--1-2--21-791--1   110001
 118 LON  INV       --2-1--1-------------41---11--------8--------41--1-   110001
  13 ALN  INC       ----2----2------91-----------------1------88--78---2   110010
  44 CAL  CAN       ----2----2-----------16---2-----8------8--88141-94   110010
 102 GEU  MAC       ----115--1----1111111----11---12-1424413541112411   110011
  42 BRO  CIL       --------44--------11-----------------782------217121   11011
 147 POA  PAL       ------------------1-------11---1--1221-42---2-2171   11101
 149 POL  OCC       ------------------------------------2------1-----972-   111100
 130 MON  COR       -----------6---------------------2-----68-----9627   111101
 191 SEN  TRI       -----1----1--12---1----1---1------1--2-1-114-2611   11111

                    0000000000000000000000000000000000001111111111111111
                    0000000000111111111111111111111111110000000000001111
                    0000111111000000000000000000000000011000000000110001
                    011100011100000000000111111111111  000111111  001
                     01101100100000111110000000000001  011000011
                               0111101111100000000111     0011
```

Fig. 5. Enhanced output from TWINSPAN.

together, and the rows for species considered to respond most similarly to existing environmental conditions are placed close together. The closer together the more similar the relationship. The single-digit value in the table for each species for a give releve is a code for the cover class that included the absolute cover estimated for that species on that releve. These are the cover classes used: 1 - 1-2%, 2 - 3-6%, 3 - 7-9%, 4 - 10-14%, 5 - 15-19%, 6 - 20-29%, 7 - 30-49%, 8 - 50-69% and 9 - 70-100%. (The discussion of the species will be given later in this chapter.)

TWINSPAN is a divisive classification. The 0's and 1's in the rows at the bottom (which refer to releves) and right-hand side (which refer to species) of the analysis are used to interpret the separation into classes. Each row illustrates the division of releves into different classes at the first through sixth levels of separation. For example, the first row has 34 0's followed by 15 1's. This means that Releves 45 through 14 were different than Releves 9 through 41. The program also provided an eigenvalue of 0.353 to suggest the strength of that difference. The second row shows the division of 34 releves into 2 classes (Releves 45 through 18 and 37 through 14) with an eigenvalue of 0.365 and the division of 15 releves into 2 classes (9 through 25 and 1 through 41) with the eigenvalue of 0.414. Eigenvalues in this range would not indicate a particularly strong separation. (Eigenvalues generated in TWINSPAN and DCA are standardized and may be viewed similar to r^2 as an expression of the percent of the overall variation explained by that axis. Personal communication with Robert Keane.) (The remaining rows continue through 6 levels of division.)

I enhanced the TWINSPAN output by listing the respective class code for each of the 2 models and 2 gradients used in the analysis above each of the releve columns. The fact that these releves did not have strong separations is borne out by the model and gradient codes at the top of Fig. 5. The wide distribution of most of the codes for each gradient and model along the range of releves confirms the lack of distinct classes in most cases. However, a few patterns emerged that merit comment. In the riparian model, most avalanche releves (code=1) are clustered in the middle within 40% of the range of all releves. For the cover model, the conifer releves (code=1) are grouped in the left third of the output. Releves with tall shrubs (code=5) are grouped in 2 separate but relatively tight patterns. The mature H. lanatum cover gradient showed less pattern of separation than any of the others. I interpret this as an indication that little ecological explanantion can be based solely on abundance by cover of mature H. lanatum. However, many of the lowest cover class are at the left side and associated with conifer canopies. The values for the New-Young-Mature Abundance Cube gradient are widely dispersed with the exception of the 6 releves of the most abundant cell (code 6) which occur within a third of the releves at the right side. Three of the 6 NYMABUNC code=6 releves were associated with tall shrubs, but none of the 6 releves were associated with avalanches or conifers.

DCA

This method also ordinates both samples and species at the same time without subjective bias of the ecologist to weight the species or select the end releves. Additionally, DCA has the advantage of calculating multiple axes of gradients represented in the data. I used output from axis 1 (eigenvalue=0.638), axis 2 (eigenvalue=0.513) and axis 3 (eigenvalue=0.387) to project the 49 samples into a 3-dimensional space (Fig. 6). The axes represent a single gradient or combinations of gradients. However, the interpretation of which gradient or gradients is represented by each axis is left to the researcher. Each axis is labled in units of standard deviation; a single unit equals 0.01 of a standard deviation. There is a known distance between any two species or samples on a given axis. Various classes of the two cover and two gradient models were superimposed on the base ordination. The absolute cover values for each species was used for this DCA rather than coding the cover as in TWINSPAN.

For the cover model, the 8 releves with conifer cover occupied the upper fourth of axis 1 and the middle third of axis 3 while filling essentially the entire length of axis 2. Other groups in this model were not as diagnostic. However, conifer openings (n=5) were restricted to the middle third of axis 1 (Fig. 7). All of the tall shrubs and hardwoods were positioned in the lower half of axis 1 and for the most part in the lower third of axis 3 although distributed over most of the length of axis 2. The DCA did give a good separation between conifer cover and those releves with cover from deciduous trees or tall shrubs.

The avalanche group in the riparian model forms a notable group of samples that occupy the middle third of axis 1 and more than two-thirds of both axes 2 and 3 (Fig. 7). Again, the ordination clustered a group of samples with a common landform/riparian feature: avalanche runout

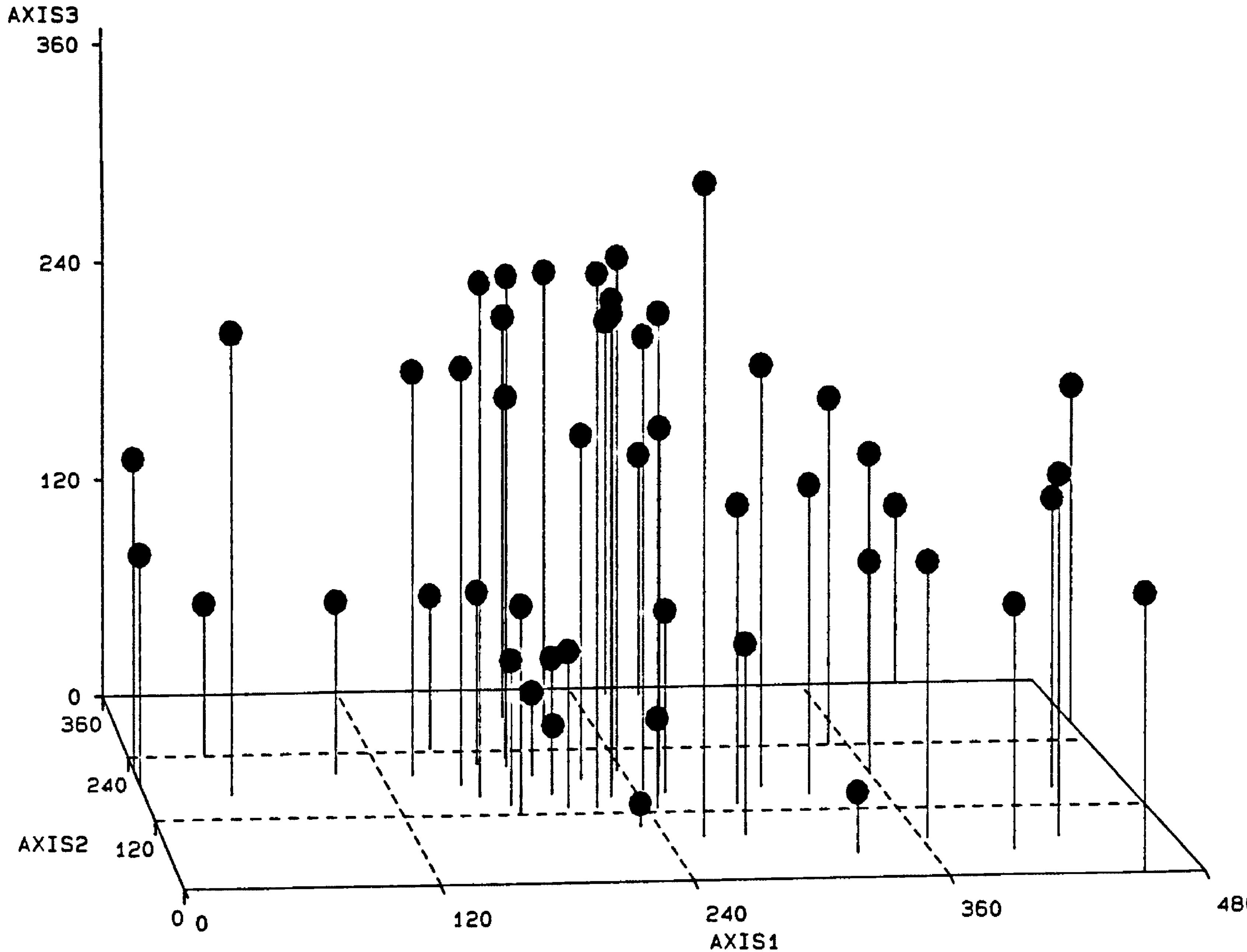

Fig. 6. DCA of all 49 releves derived from all species combined.

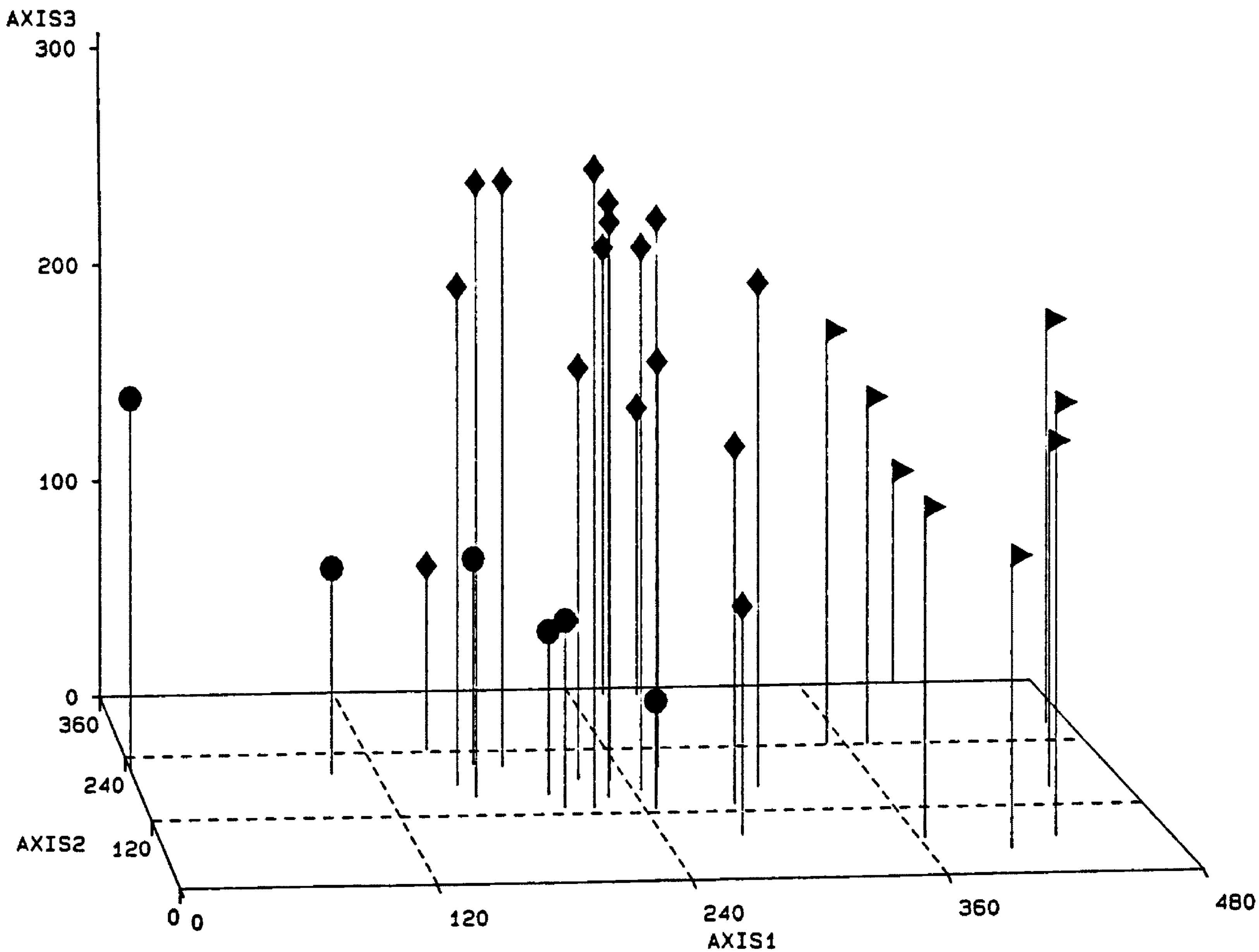

Fig. 7. Overlay of all releves in NYMABUNC=6 (●), avalanche (◆), and conifers (▶) on the DCA graph of all releves as shown in Fig. 6.

zones. On the other hand, several other samples that were not avalanches were placed within the same ordinational cloud. The two other groups in this model, streamside riparian and other riparian, did not cluster into distinctive groups.

The samples in each of the five classes of the mature _H. lanatum_ cover gradient did not form distinct groups or clouds in the DCA output. Cover of mature _H. lanatum_ alone is not an indicator of ideal sites.

By far the tightest clouds formed occurred with overlays of the new-young-mature abundance cube gradient (NYMABUNC). Releves of the most abundant group (NYMABUNC-6) formed a narrow, elongated ellipsoid cloud with the concentration of points in the lower part of the middle third of all 3 axes. Another good pattern occurred for NYMABUNC-4 in the middle third of axes 1 and 2 but along most of axis 3. These two clusters of samples reinforced the likelihood that the abundance cube concept may be an acceptable way of interpreting the data.

Percent Organic Matter

Values for percent organic matter ranged from 4% to 71% with a mean of 19%. However, releves 24 and 25 were atypical for this factor. When their respective values of 70% and 71% are excluded the range is 4% to 38% and the mean is 17% for the 49 releves. At the beginning of this study, I felt percent organic matter might be an evironmental indicator that could be related to the amount of available moisture on the site during the growing season. Sites with more moisture might produce more biomass that could result in higher amounts of organic matter. These data neither prove nor disprove that relationship. However, percent organic matter did not prove useful to separate any of the categories in the models and gradients analyzed. The means for percent organic matter in each category of the models and gradients is shown in Table 7. Standard deviations are sufficiently large that none of the groups would be considered different from the other. Percent organic matter was not diagnostic in predicting or characterizing sites with abundant H. lanatum.

Soil Texture

The standard texture triangle has 12 classes for mineral soils. Four of those classes (clay, sandy clay, silty clay and silt) did not occur in the 49 soil profiles in this study. For the purposes of this study, the remaining 8 classes were divided into 15 classes. In addition, horizons with organic matter >/= 20% are considered organic soils rather than mineral soils and are not given a texture class. Fig. 8 illustrates the texture for each of the horizons in the 49 soil profiles. At least 11 of the profiles had horizons with 1 of the 3 classes of sand present and were considered to be well drained. Nearly 40% of the releves had organic soil rather than mineral soil in the top horizon. If soils are high in organic matter, textures are difficult to determine. This helped me to understand why I had experienced so much difficulty in attempting to determine soil textures in the field.

When I analyzed the various models and gradients in this study, neither the presence nor absence of an organic horizon at the surface nor a sandy substrate was diagnostic for the abundance of H. lanatum.

Table 7. Mean values for environmental factors for all releves and each model category and gradient class.

Category/Class	n	Elevation (ft)	Aspect	Slope (%)	Area (a)	Soil Organic Matter (%)	Mature HERLAN Cover (%)
All	49	4,215	178	15	0.6	19	23
COVERMOD							
Conifer	8	4,385	218	10	0.3	24	5
Conifer Cut	3	4,633	197	10	0.6	14	6
Conifer Opening	6	3,675	133	17	0.2	11	21
Hardwood Trees	2	3,520	168	4	1.5	16	53
Tall Shrubs	10	4,207	174	14	0.3	26	34
Other - NA	20	4,320	175	18	0.9	18	25
RIPARMOD							
Avalanche	16	4,649	150	28	0.9	24	20
Streamside	15	3,831	213	3	0.4	19	30
Other Riparian	8	4,291	187	16	0.4	19	19
Other - NA	10	4,036	166	11	0.5	13	20
HELACOVC							
HELACOVC-1	10	4,344	231	16	0.2	21	4
HELACOVC-2	9	3,943	155	18	0.8	15	7
HELACOVC-3	9	4,728	161	18	0.5	28	12
HELACOVC-4	13	4,115	175	14	0.7	18	29
HELACOVC-5	8	3,946	165	6	0.5	14	68
NYMABUNC							
NYMABUNC-1	8	4,215	190	18	0.3	17	6
NYMABUNC-2	4	4,623	211	28	0.4	15	10
NYMABUNC-3	16	4,329	178	14	0.6	25	7
NYMABUNC-4	12	4,133	151	15	0.8	18	39
NYMABUNC-5	3	4,360	212	15	0.8	15	38
NYMABUNC-6	6	3,730	173	3	0.6	13	58

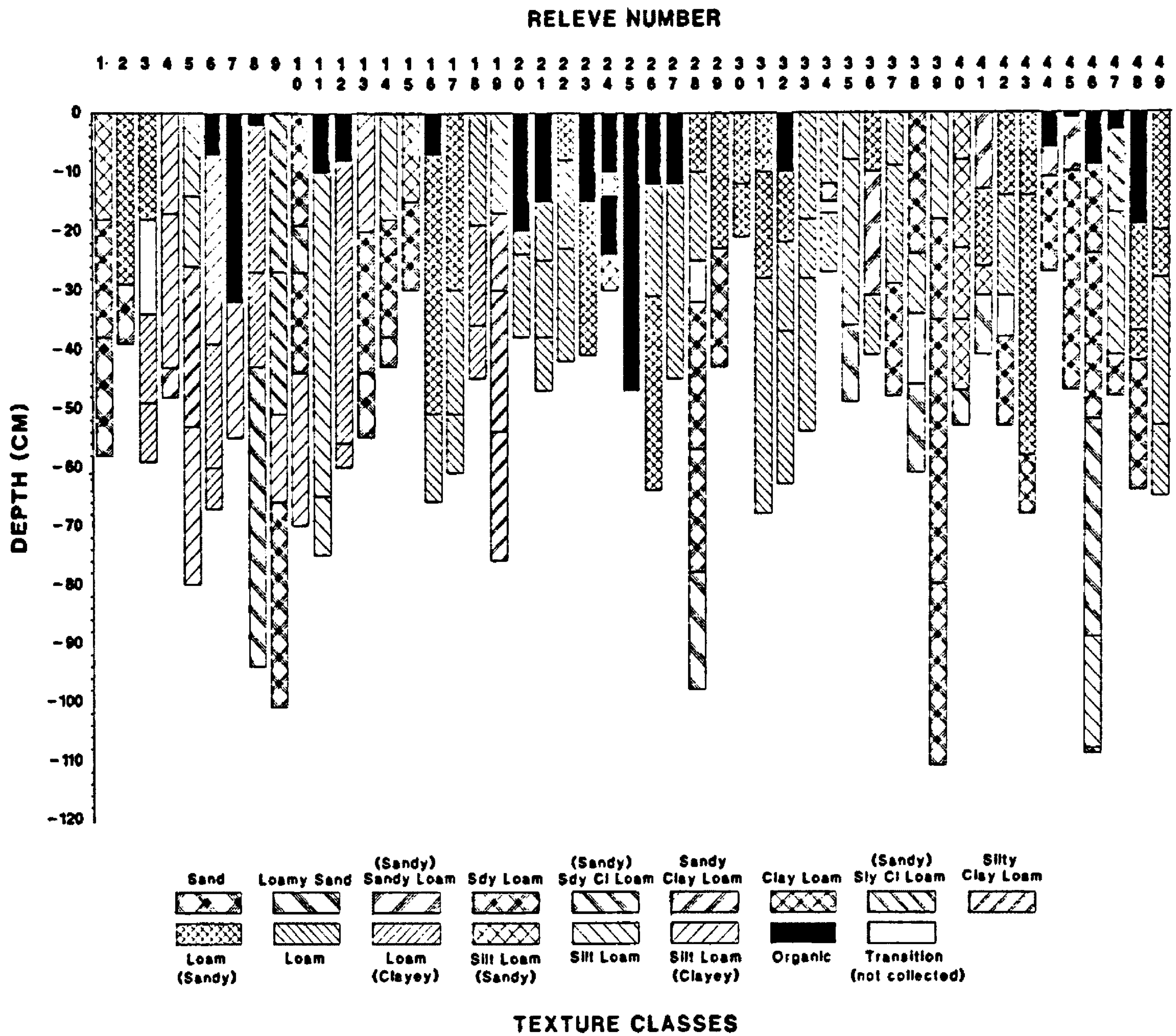

Fig. 8. Soil profiles by soil texture class and horizon depth.

In fact, the 6 releves in the NYMABUNC cell 6 had horizons with 8 of the 15 texture classes of mineral soil which ranged widely from sand to silt loam. Only plot 11 had an organic surface horizon, but the mature cover for *H. lanatum* was 80%. Although only one of the 6 abundant releves had organic soil, the abundances for new, young and mature *H. lanatum* in that releve were in the highest class (5) for each respectively. An organic horizon is not required but it certainly did not limit the abundance of *H. lanatum*.

Aspect and Elevation

A full range of aspects was represented among the 49 releves. Aspects varied from 40 to 355 degrees, but nearly 45% of the samples had a south or southeast aspect. Elevations for the releves ranged from 2,340 to 5,640 ft with a mean of 4,215 ft. Seventy-five percent of the releves occurred between 3,000 and 5,000 ft elevation. However, in examining the results of pattern analysis and the 2 models and 2 gradients, I feel that neither aspect nor elevation were environmental factors that substantially influenced the abundance of *H. lanatum*.

Tall Shrubs

Better understanding of the ecological factors involved became more apparent when a subset of the releves that share a common characteristic are separately ordinated (Gauch 1982). This approach proved helpful in the case of the tall shrub class of the cover model. Ten releves were identified as tall shrubs. However, releve 17 was excluded from this analysis because it was an outlier; it was the only releve in the study growing on a roadfill and was quite atypical from the other tall shrub plots. The DCA for this subset resulted in 4 releves grouped near the center (Fig. 9). Eigenvalues for axis 1 and axis 2 were 0.681 and 0.403, respectively. Closer inspection of coverages of species revealed a relationship between abundant H. lanatum and high coverages of Alnus incana. This pattern suggests that where the ecological distributions of H. lanatum coincide with abundant concentrations of A. incana, H. lanatum is often abundant also. Indeed, my feeling is that A. incana may be one of the key ecological equivalents to indicate microsites where H. lanatum might thrive. This information provides a transition to the discussion of the study's second objective: to identify species which respond to the environment in ways similar to H. lanatum.

Ecological Equivalents

Three different analysis procedures provided results for species that were closely associated with H. lanatum. The results generated might stand alone or be considered together. These three approaches were DCA, TWINSPAN, and a synthesis of several constancy/coverages values for species. The strength of DCA and TWINSPAN are different, yet they yield complementary results (Table 8). Additionally, table work was used to identify those species that might be most indicative of ideal areas within a certain group of a particular model or gradient.

Table Work

The entire association table for species coverage contained 230 species and 49 releves. These 230 species were supported with nearly

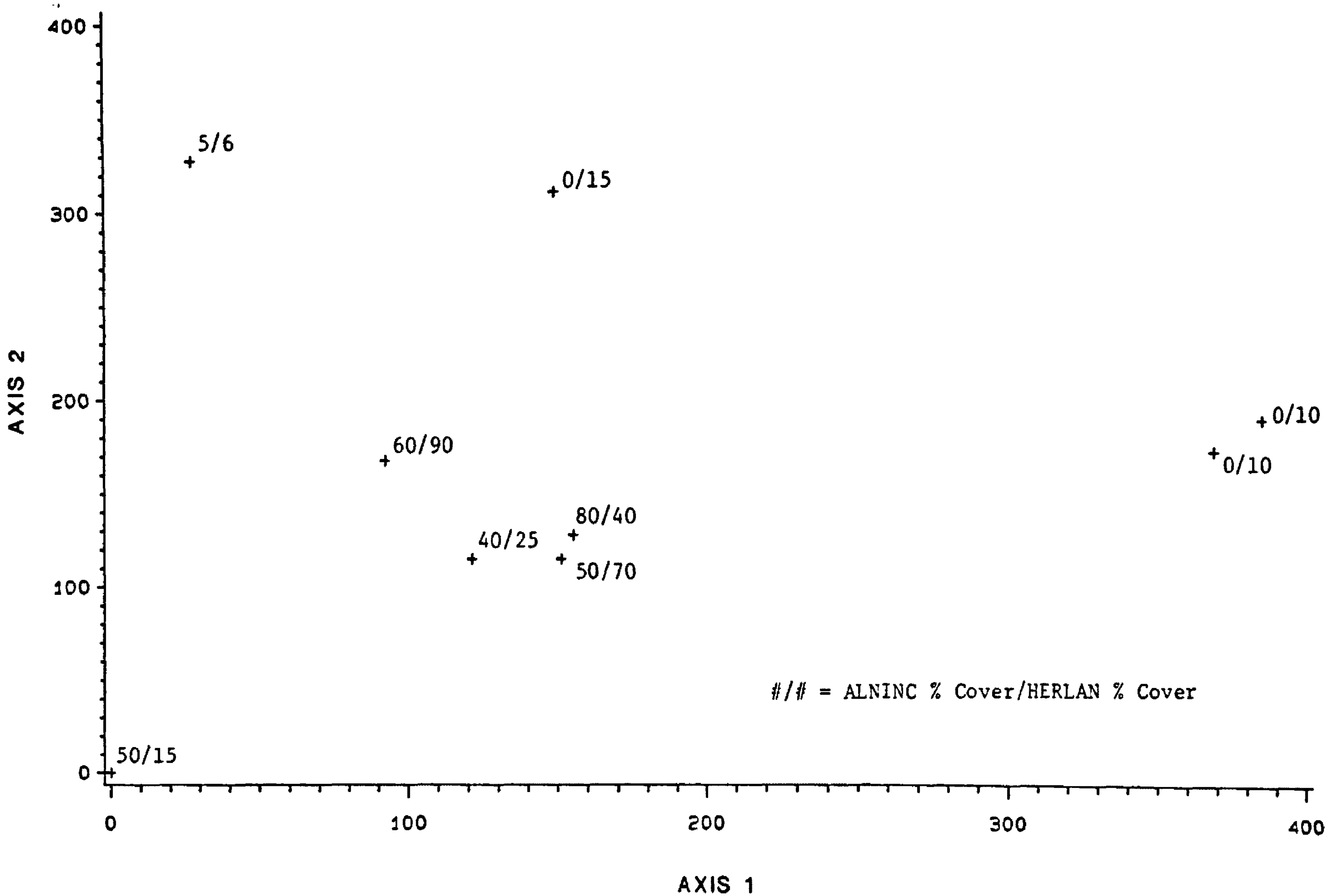

Fig. 9. DCA for the tall shrubs set with percent cover shown at each releves for Alnus incana and H. lanatum.

Table 8. Plant species (ecological equivalents) commonly associated with *H. lanatum*.

Scientific Name	Common Name	DCA	TWINSPAN
* Alnus incana	Thinleaf Alder	x	x
+ Angelica arguta	Sharptooth Angelica		x
Aster modestus	Few-flowered Aster	x	
Bromus ciliatus	Fringed Brome	x	
* Calamagrostis canadensis	Bluejoint Reedgrass	x	x
* Carex bebbii	Bebb's Sedge	x	x
Cinna latifolia	Drooping Woodreed		x
*+ Elymus glaucus	Blue Wild Rye	x	x
+ Epilobium angustifolium	Fireweed	x	
+ Equisetum arvense	Field Horsetail		x
Festuca subulata	Bearded Fescue	x	
Galium triflorum	Sweetscented Bedstraw	x	
*+ Geum macrophyllum	Large-leaved Avens	x	x
Lonicera involucrata	Bearberry Honeysuckle		x
Pteridium aquilinum	Brakenfern		x
*+ Rubus idaeus	Red Raspberry	x	x
*+ Urtica dioica	Stinging Nettle	x	x
Veratrum viride	Green False Hellebore	x	
+ Viola canadensis	Canada Violet	x	

* Species that are common on both lists.

+ Species deemed to have broad ecological amplitude in these 49 releves.

DCA is taken from the list of 38 species with constancies >/= 25%; *A. incana* at 20% constancy is an exception.

TWINSPAN is taken from the reduced list of 48 species and *C. bebbii*.

450 verified voucher specimens collected from the releves (see Appendix). In order to reduce the species list to a more workable number and identify the important species to consider, I generated a single constancy/coverage list for all releves combined. Eighteen species had constancies >/= 40%, 11 species had values of 30-39%, and 8 species had values of 25-29%. This provided a working list of 37 species that occurred frequently in the releves. Later, two additional species were added for a total of 39. Alnus incana, with a constancy/coverage of 20% / 30% for the 49 releves, was added because of its dominance in the tall shrub and streamside releves. Likewise, Montia cordifolia was added because of its constancy/coverage of 47% / 32% in the streamside group.

DCA

I used DCA as an analytical tool to help determine which species respond to the environment similarly to H. lanatum. This method ordinates the species simultaneously with the samples. This time axis 1 and axis 2 were used; their eigenvalues were the same as discussed earlier in the DCA for the releves. The 14 species I selected from DCA are marked in Table 8.

I used the 37 species mentioned above plus A. incana and examined their values on the 2 axes (Fig. 10). The arbitrary decision was made to select only those species that were within plus or minus one standard deviation from H. lanatum on each axis. I allowed minor exceptions for 5 of the species: Bromus ciliatus, Epilobium angustifolium, Festuca subulata, Urtica dioica, and Veratrum viride. This was subjective but

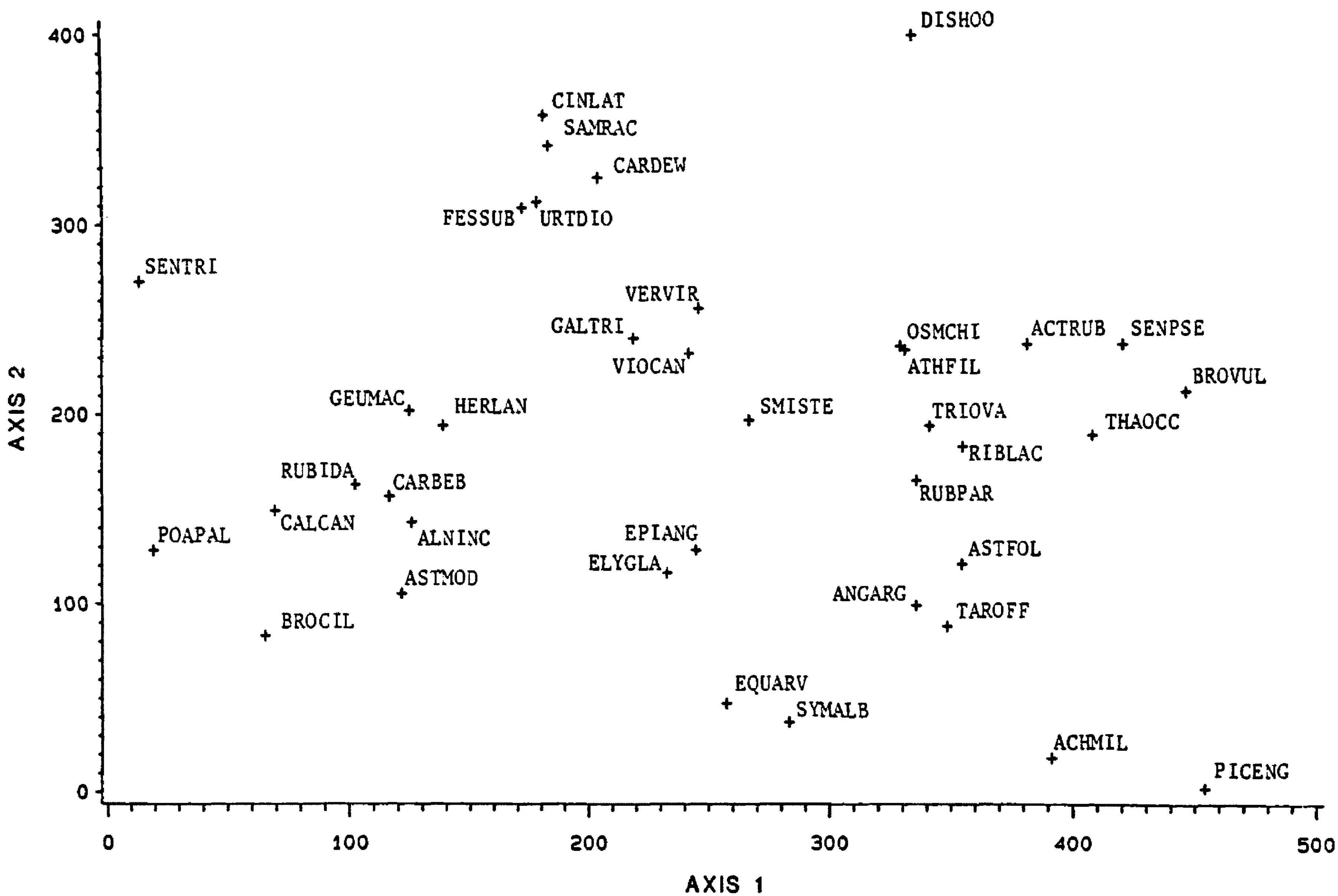

Fig. 10. DCA for the 38 species with frequent occurrence.

seemed ecologically sound. Based solely on this DCA, the 5 species that were most ecologically equivalent to *H. lanatum* were *Geum macrophyllum*, *Carex bebbii*, *A. incana*, *Rubus idaeus* and *Aster modestus*.

TWINSPAN

Fig. 5 also shows the results for the species groups in TWINSPAN. These 48 species were selected by the program as the most important species. However, all 230 species were used to generate the output. Again species closer together are deemed to respond more similarly than species further apart. TWINSPAN shows the order in the species list, but does not show how much difference or distance is between two species. The eigenvalue for dividing the top two-thirds from the bottom third was 0.716, a strong separation. The next break between *H. lanatum* and *Equisetum arvense* had an eigenvalue of 0.468. I selected those 12 species from *Elymus glaucus* to *G. macrophyllum* as the ecological equivalents based on this method and so indicated them in Table 8. *C. bebbii* is not shown in Fig. 5 but would have been between *R. idaeus* and *U. dioica*. As I interpreted these results, I felt this sedge merited designation in TWINSPAN, as well as DCA. In the combined list, most of minor species were outside this range of the ecological equivalents. In fact, 166 species were above *E. glaucus*, and 37 species were below *G. macrophyllum*. Counting the minor species also, there were only 27 species from *E. glaucus* to *G. macrophyllum*.

Some additional information is included in Table 8 for those species identified by both DCA and TWINSPAN as responding similarly to *H. lanatum* and for those species which I felt demonstrated broad ecological amplitude in this study. A. incana, C. canadensis and C. bebbii are the only species selected from both DCA and TWINSPAN that do not have broad ecological amplitude. Also, about the same number of species were selected by DCA and TWINSPAN.

Note of Caution

A caution must be expressed about placing complete and unreserved confidence in the list of ecological equivalents. To be ecological equivalents in the truest sense, two species would have identical ecological distributions. These species were detected from patterns in the data from this study's 49 releves. These samples come from a small area of the much larger geographic range of H. lanatum. Ideally, these samples would represent the full ecological range of H. lanatum within the geographic area of the study. In reality that is not possible. For this approach to merit complete confidence, the entire ecological distribution of H. lanatum would need to be represented in the samples. Furthermore, to understand what portion of the ecological distribution of the target species coincides with that of the indicator or ecological equivalent, it would be necessary for the samples in the study to represent the full ecological distribution for all ecological equivalents. That would be beyond the scope and means of most, if not all, studies. Therefore, caution must be used when suggesting certain species might indicate sites suitable for another species. Nevertheless, the species listed as "ecological equivalents" may serve admirably in determining sites suitable for H. lanatum. Better results would be expected, if not one but several of the ecological equivalents grew on the target site.

Absence of Species

Another way to glean information from these data is to recognize the lack of some prominent species. In these 49 releves, *Larix occidentalis* occurred on only two releves with 1% and 5% cover; *Pseudotsuga menziesii* had 1% cover in one releve. Some series in the Montana forest habitat types are too dry for *H. lanatum*. *P. menziesii* is the conifer species in Montana most sensitive to moisture; as moisture availability increases it is usually the first conifer to be excluded from sites (personal communication Dr. Robert Pfister). *Salix* was not abundant in these 49 releves. On the other hand, Mace (1984) reported a *Salix* spp. flat vegetation type in the floodplain complex where the constancy for *H. lanatum* was 73%. However, the mean cover for *H. lanatum* in the *Salix* spp. v.t. was only 4%. Most of these 49 releves had coverages for *H. lanatum* much greater than the types of sites reported by Mace. Based on the releves in my study, *H. lanatum* does not grow abundantly under *Salix*.

General Discussion

Interpretation of Results in Relation to Original Hypotheses

It would be an oversight not to comment on the original hypotheses set forth in the study plan. Curve A in Fig. 4 depicted that mature *H. lanatum* cover would decrease with less disturbance. Based on these 49 releves, sites did not have high abundance of *H. lanatum* as a function of disturbance in general but rather in association with depositional disturbance.

Curve B represented a soil texture gradient. This hypothesis is true only with respect to very fine soils. None of the samples from the 49 profiles had textures of clay, sandy clay, silty clay or silt. However, *H. lanatum* seemed to occur with equal abundance on soils in most other texture classes. Certainly, sandy soils did not hinder the abundance of *H. lanatum*.

Curve C modelled the expected results of increased soil moisture. For this study, I attempted to demonstrate a relationship between soil moisture available to the site throughout the year and the percent organic matter in the top 10 cm of soil. There may or may not be a connection between these two factors. However, *H. lanatum* abundance (coverage of mature plants) did not correlate with percent organic matter.

A light gradient is represented by Curve D. These data suggest this hypothesis is not entirely correct. If the shade is a result of conifer canopies it appears to be true, but the curve is not true for hardwood canopies. For example, *H. lanatum* can thrive under canopies of *Populus tremuloides*, *Populus trichocarpa* or *Alnus incana*.

The last gradient, grazing, is illustrated with Curve E. Only two of the releves had any evidence of grazing from domestic livestock, and another two had heavy wildlife utilization. I did not see enough evidence of grazing to justify comment on this factor based on the releves in this study.

It was valuable to have several hypotheses in mind when I began this study. As a result of the data collection and/or data analysis, these ideas are modified in major or minor ways. A benefit of this study would be the potential to now propose new hypotheses that could be tested in future studies.

New and Young Reproduction

Data for the same variables were collected for both the new and young reprodution. Two types of data were used to characterize the immature H. lanatum plants: microenvironment and plant. Percent cover estimates of the microsite (20 cm diameter circle) immediately surrounding each individual were analyzed for litter, bare soil, moss/lichen, herbaceous cover less than 50 cm and woody cover less than 50 cm. The plant variables were leaf length, root length, crown diameter and dry weight of the top and the root. The results are summarized for new and young reproduction in Table 9 and Table 10, respectively. Each table shows the mean value for each variable for all new or young combined and then subdivides the data into each of the classes for the 2 models and 2 gradients.

I reported only the mean values since the low number of samples and the generally large standard deviations were such that significant differences were not expected. However, the range of values for each variable does indicate the magnitude of differences observed. For new reproduction (n=112 out of a potential 196), leaf length ranged from 28 to 207 mm, root length 10 to 75 mm, crown diameter 1 to 5 mm, top dry weight 0.001 to 0.048 g and root dry weight 0.001 to 0.195 g. The young

Table 9. Mean values for new reproduction for entire study and each model category and gradient class.

Model/ Gradient	Poten n	n	Litter	Bare Soil	Moss/ Lichen	Herbs LT50cm	Woody LT50cm	Leaf Len	Root Len	Crn Dia	Top Dwt	Root Dwt
			Percent					mm			g	
All	196	112	63	4	33	68	23	83	27	2	0.007	0.017
COVERMOD												
Conifer	32	17	73	1	26	46	15	80	25	2	0.007	0.016
Conifer Cut	12	4	88	0	12	83	33	77	36	2	0.005	0.017
Conifer Opening	24	22	44	3	53	74	10	101	32	3	0.012	0.035
Hardwood Trees	8	4	91	0	9	80	4	68	22	1	0.004	0.008
Tall Shrubs	40	26	56	11	33	61	29	81	27	2	0.007	0.013
Other - NA	80	39	69	3	28	77	30	79	25	2	0.006	0.011
RIPARMOD												
Avalanche	64	25	87	5	8	60	40	77	24	2	0.005	0.011
Streamside	60	44	56	4	40	70	19	86	27	2	0.008	0.015
Other Riparian	32	22	43	6	51	73	20	78	27	2	0.007	0.017
Other - NA	40	21	71	1	28	70	13	92	31	2	0.010	0.031
HELACOVC												
HELACOVC 1	40	16	38	3	59	49	7	102	35	3	0.015	0.047
HELACOVC 2	36	15	62	0	38	65	14	79	23	2	0.006	0.015
HELACOVC 3	36	25	77	2	21	61	30	75	29	2	0.005	0.013
HELACOVC 4	52	34	84	4	12	77	28	83	24	2	0.006	0.011
HELACOVC 5	32	22	35	9	56	81	24	83	26	2	0.007	0.012
NYMABUNC												
NYMABUNC 1	32	4	51	0	49	90	15	92	27	2	0.007	0.016
NYMABUNC 2	16	16	55	4	41	58	35	71	25	2	0.005	0.012
NYMABUNC 3	64	36	66	1	33	55	13	89	31	2	0.010	0.029
NYMABUNC 4	48	30	72	5	23	79	36	74	23	2	0.005	0.009
NYMABUNC 5	12	3	86	2	12	67	28	70	21	1	0.004	0.004
NYMABUNC 6	24	23	53	8	39	79	14	95	29	2	0.009	0.016

Table 10. Mean values for young reproduction for entire study and each model category and gradient class.

Model/ Gradient	Poten n	n	Litter	Bare Soil	Moss/ Lichen	Herbs LT50cm	Woody LT50cm	Leaf Len	Root Len	Crn Dia	Top Dwt	Root Dwt
			Percent					mm			g	
All	196	127	66	7	27	59	18	575	242	17	1.86	6.97
COVERMOD												
Conifer	32	19	81	0	19	27	3	646	270	19	2.69	7.68
Conifer Cut	12	10	81	0	19	69	9	608	415	20	2.40	14.42
Conifer Opening	24	17	43	3	54	64	21	515	174	14	1.42	3.89
Hardwood Trees	8	8	73	11	16	38	24	576	142	15	1.31	2.80
Tall Shrubs	40	31	54	16	30	60	15	588	194	15	1.36	3.37
Other - NA	80	42	73	4	23	73	26	550	271	20	2.01	9.57
RIPARMOD												
Avalanche	64	36	85	7	8	68	22	628	255	20	2.27	9.97
Streamside	60	44	55	10	35	55	13	538	220	15	1.65	4.60
Other Riparian	32	21	52	0	48	55	23	531	230	17	1.61	5.81
Other - NA	40	26	71	5	24	56	16	600	273	18	1.85	7.76
HELACOVC												
HELACOVC 1	40	27	66	2	32	37	17	636	284	19	2.63	9.59
HELACOVC 2	36	20	62	2	36	70	9	554	295	21	2.46	11.54
HELACOVC 3	36	25	82	5	13	59	17	684	299	20	2.27	9.03
HELACOVC 4	52	31	74	6	20	63	23	473	177	14	1.04	3.01
HELACOVC 5	32	24	42	17	41	69	19	542	176	15	1.12	3.16
NYMABUNC												
NYMABUNC 1	32	10	66	0	34	58	23	687	293	22	1.94	11.42
NYMABUNC 2	16	6	72	2	26	29	72	819	363	22	3.92	13.60
NYMABUNC 3	64	56	71	4	25	56	7	600	285	19	2.40	9.28
NYMABUNC 4	48	19	61	5	34	76	27	456	196	15	0.96	3.65
NYMABUNC 5	12	12	83	3	14	59	13	642	194	16	1.66	3.61
NYMABUNC 6	24	24	48	20	32	61	21	472	153	13	0.88	2.36

reproduction (n=127 out of a potential 196) had ranges of 159 to 1,031 mm for leaf length, root length 22 to 905 mm, crown diameter 6 to 32 mm, top dry weight 0.08 to 8.42 g and root dry weight 0.10 to 33.15 g. For both the new and the young plants, means for the plant variables were reasonably uniform for each of the classes given the tremendous variation as noted in the ranges. It did not really matter what the group or class was, the new and young _H. lanatum_ grew about the same.

Regarding the cover for the immediate area surrounding the plants, possibly the only variable that stands out in all of the gradients for both new and young is bare soil. Those classes of releves with abundant _H. lanatum_ (tall shrubs, hardwood trees, HELACOVC-5 and NYMABUNC-6) also had higher percent cover for bare soil. The exception to this is the class hardwood trees which had 53% cover for _H. lanatum_, but zero for bare soil for the new reproduction. I give this as an observation without any attempt to offer an explanation.

Without a doubt the greatest benefit from the new and young reproduction portion of the study came during the data collection. The fact that I looked intently for 4 individuals of each type on each releve caused me to examine the releves and the individual _H. lanatum_ plants with greater detail than I would have done otherwise. It was during this part of the data collection that I began to know this species with much more familiarity.

Onset of Growth

I suspect day length is the triggering mechanism and the rate of growth is influenced by temperature. I assume temperature is an important factor controlling the onset and rate of growth though a combination of the other environmental factors would also have an influence. This suggests to me that the interaction between temperature and photoperiod influences the beginning of shoot development. That is, up to a point warming temperatures alone may cause shoot growth to begin. However, if temperatures remain cool (e.g., 32 degrees because of an unusually late snow pack) then growth will also begin once the day length reaches a certain point. It seems logical that the interaction of temperature and day length control the beginning of shoot growth. I have observed that new *H. lanatum* shoots are susceptible to heavy frosts but feel the new shoots are able to tolerate some frosts early in the growing season. Growth and flowering show an elevational lag which may be linked to temperature.

Response to Fire

In my opinion, *H. lanatum* should be able to survive most fires and would initiate growth and send up shoots from the root crown either in the same season or the following year. I observed areas in Yellowstone National Park where fire had burned the site the previous year, but mature *H. lanatum* were growing well. Also, the species typically grows in riparian microsites and would be protected naturally from lethal temperatures in most fires.

Establishment in Closed Communities

How did *H. lanatum* become established in some otherwise closed communities, especially ones of dense grass? Why are mature plants of

H. lanatum there to begin with? These areas often occur in the runout zones of avalanche chutes and snowslide fields. I suggest this is evidence that many individuals of this species are long-lived. Also, I submit that these areas may be subject to episodic periods of heavy depositional disturbance during some decades which may temporarily open up the community, reduce the competition from other species and provide a window of establishment for H. lanatum.

Propagation Trials

Although it was not a part of this study, I conducted a small trial to seed and transplant H. lanatum in the Poorman Creek drainage on the Kootenai National Forest about 15 miles south of Libby, Montana. Seed was sown in the fall. After 4 growing seasons, average seedling height was less than 10 cm. The root systems of small, sexually mature individuals were transplanted in the spring. Nearly 50% of the plants survived after 4 growing seasons; a couple of plants flowered during some years. Since seedling development is slow, the rationale for attempting to transplant mature plants would be to shorten the length of time required to have plants producing seed naturally on the site.

CONCLUSIONS AND RECOMMENDATIONS

Historical Perspectives

In the literature review, several sources were cited that had recommended and discussed the propagation of *Heracleum lanatum*. I am intrigued with the cyclic nature of these recommendations that have occurred at least 5 different times over the last nearly 70 years. Why did this notion seem to surface about every 15 years? For a long time, *H. lanatum* has been recognized as a highly productive and clearly palatable species. It would be wonderful to seed this species one year and in the next year or two have abundant forage 5 to 7 ft tall. The simple fact is this species is not easy to establish on new sites and develops very slowly once it is established. I submit that researchers and managers recognized the potential this species had to offer, promoted it, became disenchanted with the dismal results, and moved on to other species with more promise. Then, a decade or two later a new group of individuals started the cycle over again.

In my opinion, it will be most difficult to achieve consistent success in propagating *H. lanatum* in new areas. If successful introductions do occur, patience and persistence will be required over a period of many years to decades. Lush production will not result in a mere 2 or 3 years.

Even with the work that has been done and the recommendations that have been made over the past 7 decades, considerable misconceptions still exist about this species.

Conclusions

Sites with abundant H. lanatum usually are characterized as having some type of depositional disturbance. However, given that depositional disturbance is present, H. lanatum exhibits broad ecological amplitude and may thrive in a wide variety of types and conditions and is not constrained by elevation, aspect or most soil textures. H. lanatum seems to thrive in areas that are frequently disturbed, particularly when the disturbance is depositional, and where an additional increment of moisture is annually available. Two types of sites that meet these conditions are stream sides, especially meandering streams, and the toe slopes of avalanche chutes. Deposition of soil occurs in both situations; thus, the root systems of established plants are not disturbed. Also, extra moisture is available on both kinds of sites.

H. lanatum does not have high fidelity to any 2 or 3 habitat types or community types. The species does not grow abundantly under conifer cover and is notably absent from sites in the Pseudotsuga menziesii series of habitat types. Although growth under conifer canopy is not abundant, this species is not shade intolerant; it grows quite well under the shade of broadleaf canopies. A majority of the releves with highly abundant new-young-mature H. lanatum keyed to the Alnus incana c.t. or grew under partial shade of other broadleaf species.

I think Glacier National Park provides an ideal habitat for H. lanatum, an opportunistic species that favors disturbed area. The species grows well on streamside floodplains, fill slopes, at Logan Pass, in the runout zone of avalanche chutes, and even the well drained glacial till forested areas on the west side of the park adjacent to the

North Fork of the Flathead River. A combination of disturbed sites and additional moisture from streams, avalanches, seeps, or increased precipitation from the orographic effect of the park's mountain ranges provide suitable sites.

H. lanatum is considered highly palatable for most animal species. It is not surprising that bears (both black and grizzly) which are gross feeders would be opportunistic about seeking out this palatable species that grows rapidly early in the spring and produces abundant amounts of succulent and palatable biomass. In Glacier National Park, large populations of bears and abundant amounts of *H. lanatum* seem to coexist quite well and the bears are greatly benefited.

Clearly, other areas of northwestern Montana are well suited for *H. lanatum*, many of which are microsites. In this study, sites with highly abundant concentrations of new, young and mature *H. lanatum* combined were found in the northwestern, northeastern, and southern extensions of the study area.

Management Recommendations

1. *H. lanatum* should be protected. The species does not readily establish in new areas. Hence, those areas where *H. lanatum* is present and abundant should be managed in a way that does not compromise the existing population of *H. lanatum*. This would include refraining from activities that might alter the existing water table or moisture available to the site (e.g., road construction, etc.), large scale timber harvests in adjacent areas, and substantial increases in grazing or foraging pressures from either wild or domesticated animals

(certainly some utilization of _H. lanatum_ is acceptable and suitable). If _H. lanatum_ already grows in an area that is being harvested, limit the amount of scarification and other activities that would displace the plants' established root systems.

2. The most likely sites to introduce _H. lanatum_ either by seed or transplanting would be riparian zones, some toe slopes on avalanche chutes, and some moist openings in forests. The ideal sites would be stream-bottom floodplain microsites with undulating surfaces and slopes less than 5%.

3. Seek target sites with several of the ecological equivalents present. The greater the number of closely associated species, the more likely the site will be receptive to the introduction of _H. lanatum_.

4. In general, avoid sites with conifers present. Specifically, avoid sites with _Larix occidentalis_ or _Pseudotsuga menziesii_ or those in the _Pseudotsuga menziesii_ habitat type series.

5. If _H. lanatum_ is introduced by seed, the seed should be collected from established populations located in the same general area as the target site. It is possible that _H. lanatum_ has considerable ecotypic variability. Some of the ecotypes may require stratification to break dormancy while the seeds of other ecotypes may not need a treatment prior to germination. This is one of the reasons why it is important to collect seeds or select sexually-mature, vegetative material from areas in close proximity to where the new population will be established. The seeds should be collected when fully mature, often late August or early September, and hopefully before heavy rains have caused the seed to mold. Bad insect infestations occur during some

years, and the insects may render most seeds nonviable by feeding on the seed.

6. H. lanatum requires a cold treatment to break dormancy. This may best be accomplished by sowing the seed on the new site in the fall before the winter snows. This will mimic the natural process closely and the new seed should receive the environmental influences needed to break dormancy and permit germination the following spring. There is some evidence in the literature and some indications from my propagation of H. lanatum at Poorman Creek that the seeds have differential germination requirements and not all seeds will germinate the first or even the second year after sowing.

7. Expect extremely slow development; H. lanatum does not grow fast! It is not possible to seed H. lanatum one year and have a good cover of plants 6 feet tall by the following year. In fact, the more likely scenario with a successful seeding and normal establishment might be to have young plants 6 inches tall after 3 years. During my field work, even late in the season, I was still finding very small single-leafed new plants. This indicates the plants grow slowly and the larger young plants must be at least 2 and possible several years old.

8. Preliminary observations suggest that H. lanatum may be successfully transplanted as mature plants and may begin to set seed 2 or 3 years after transplanting. This might be the quickest way of getting seed-producing plants on the site. This species does not exhibit natural vegetative propagation and the literature is devoid of any information.

9. Areas that have seedlings and young plants developing should not be grazed or only light grazing permitted (Plummer et al. 1968).

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APPENDIX

Table A. Complete list of scientific and common names and alpha codes for all the species identified in this study.

Alpha	Scientific Name	Common Name
ABIGRA	*Abies grandis	Grand Fir
ABILAS	Abies lasiocarpa	Subalpine Fir
ACEGLA	Acer glabrum	Rocky Mountain Maple
ACHMIL	Achillea millefolium	Common Yarrow
ACOCOL	Aconitum columbianum	Columbian Monkshood
ACTRUB	Actaea rubra	Baneberry
ADEBIC	Adenocaulon bicolor	Trail-plant
AGRREP	*Agropyron repens	Quackgrass
AGAURT	*Agastache urticifolia	Nettle-leaf Giant-hyssop
AGRALB	*Agrostis alba	Redtop
AGRSCA	*Agrostis scabra	Rough Bentgrass
ALLCER	*Allium cernuum	Nodding Onion
ALNINC	*Alnus incana	Thinleaf Alder
ALNSIN	Alnus sinuata	Sitka Alder
AMEALN	Amelanchier alnifolia	Western Serviceberry
ANAMAR	*Anaphalis margaritacea	Common Pearly-everlasting
ANEMUL	*Anemone multifida (?)	Cliff Anemone
ANGARG	Angelica arguta	Sharptooth Angelica
ANTRAC	*Antennaria racemosa	Raceme Pussytoes
AQUFLA	*Aquilegia flavescens (?)	Yellow Columbine
AQUILE	Aquilegia spp.	Columbine
ARAGLA	*Arabis glabra	Towermustard
ARAHOL	*Arabis holboellii	Holboell's Rockcress
ARANUD	Aralia nudicaulis	Wild Sarsaparilla
ARCMIN	*Arctium minus	Common Burdock
ARNCOR	Arnica cordifolia	Heartleaf Arnica
ARNLAT	*Arnica latifolia	Broadleaf Arnica
ASACAU	*Asarum caudatum	Wild Ginger
ASTCON	*Aster conspicuus	Showy Aster
ASTFOL	*Aster foliaceus	Leafy Aster
ASTLAE	*Aster laevis	Smooth Aster
ASTMOD	*Aster modestus	Few-flowered Aster
ASTERX	Aster spp.	Aster
ASTROB	*Astragalus robbinsii	Robbins' Milkvetch
ATHFIL	*Athyrium filix-femina	Ladyfern
BARORT	*Barbarea orthoceras	American Wintercress
BERREP	Berberis repens	Creeping Oregongrape
BETOCC	*Betula occidentalis	Water Birch
BOTVIR	*Botrychium virginianum	Rattlesnake Fern
BOYMAJ	*Boykinia major	Greater Boykinia
BROCAR	*Bromus carinatus	Mountain Brome
BROCIL	*Bromus ciliatus	Fringed Brome
BROVUL	*Bromus vulgaris	Columbia Brome

* - voucher specimen collected
? - most probable identification based on reference material collected

Table A. Continued.

Alpha	Scientific Name	Common Name
CALCAN	*Calamagrostis canadensis	Bluejoint Reedgrass
CALRUB	Calamagrostis rubescens	Pinegrass
CAMROT	*Campanula rotundifolia	Lady's-thimble
CARBAC	*Carex backii	Back's Sedge
CARBEB	*Carex bebbii (?)	Bebb's Sedge
CARDEW	*Carex deweyana	Dewey's Sedge
CARDIS	*Carex disperma	Softleaved Sedge
CARGEY	Carex geyeri	Elk Sedge
CARROS	*Carex rostrata	Beaked Sedge
CARSTI	*Carex stipata	Sawbeak Sedge
CAREXX	*Carex spp.	Sedge
CASMIN	Castilleja miniata	Scarlet Paintbrush
CERVUL	*Cerastium vulgatum	Common Chickweed
CHIUMB	Chimaphila umbellata	Common Prince's-pine
CHRLEU	*Chrysanthemum leucanthemum	Oxeye-daisy
CINLAT	*Cinna latifolia	Drooping Woodreed
CIRALP	*Circaea alpina	Enchanter's Nightshade
CIRARV	*Cirsium arvense	Canada Thistle
CIRBRE	*Cirsium brevistylum	Short-styled Thistle
CIRHOO	*Cirsium hookerianum	Hooker's Thistle
CIRVUL	*Cirsium vulgare	Bull Thistle
CLECOU	*Clematis columbiana	Columbia Clematis
CLIUNI	Clintonia uniflora	Queen's Cup
COLPAR	*Collinsia parviflora	Small-flowered Blue-eyed Mary
COLLIN	*Collomia linearis	Narrow-leaf Collomia
CORCAN	Cornus canadensis	Bunchberry
CORSTO	*Cornus stolonifera	Red Osier Dogwood
CRADOU	*Crataegus douglasii (?)	Black Hawthorn
CYSFRA	*Cystopteris fragilis	Brittle Bladderfern
DACGLO	Dactyllis glomerata	Orchard-grass
DELOCC	*Delphinium occidentale	Western Larkspur
DESRIC	*Descurainia richardsonii	Richardson's Tansymustard
DISHOO	*Disporum hookeri	Hooker Fairy-bell
DISTRA	*Disporum trachycarpum	Wartberry Fairy-bell
DRASTE	*Draba stenoloba (?)	Slender Draba
DRYFIL	*Dryopteris filix-mas	Malefern
ELYGLA	*Elymus glaucus	Blue Wild Rye
EPIANG	Epilobium angustifolium	Fireweed
EPIGLN	*Epilobium glandulosum	Common Willow-herb
EPIPAN	*Epilobium paniculatum	Autumn Willow-herb
EQUARV	Equisetum arvense	Field Horsetail
EQUHYE	*Equisetum hyemale	Scouring Rush
EQUISE	Equisetum spp.	Horsetail

* - voucher specimen collected
? - most probable identification based on reference material collected

Table A. Continued.

Alpha	Scientific Name	Common Name
ERIACR	*Erigeron acris	Bitter Fleabane
ERIPER	*Erigeron peregrinus	Subalpine Daisy
ERISPE	*Erigeron speciosus	Showy Fleabane
ERYGRA	*Erythronium grandiflorum	Glacier-lily
FESOCC	*Festuca occidentalis	Western Fescue
FESRUB	*Festuca rubra	Red Fescue
FESSUB	*Festuca subulata	Bearded Fescue
FRAVES	Fragaria vesca	Woods Strawberry
FRAVIR	*Fragaria virginiana	Virginia Strawberry
GALBOR	*Galium boreale	Northern Bedstraw
GALTRF	*Galium trifidum	Small Bedstraw
GALTRI	Galium triflorum	Sweetscented Bedstraw
GENAMR	*Gentiana amarella	Northern Gentian
GERVIS	Geranium viscosissimum	Sticky Geranium
GEUALE	*Geum aleppicum	Yellow Avens
GEUMAC	*Geum macrophyllum	Large-leaved Avens
GLYELA	*Glyceria elata	Northern Mannagrass
GLYSTR	*Glyceria striata	Fowl Mannagrass
GOOOBL	*Goodyera oblongifolia	Western Rattlesnake-plantain
GYMDRY	*Gymnocarpium dryopteris	Oakfern
HABDIL	*Habenaria dilatata	White Bog-orchid
HACMIC	*Hackelia micrantha	Blue Stickseed
HERLAN	*Heracleum lanatum	Cow Parsnip
HIEALE	*Hieracium albertinum (?)	Western Hawkseed
HIEALB	*Hieracium albiflorum	White Hawkseed
HYPPER	*Hypericum perforatum	Klamath Weed
LACBIE	*Lactuca biennis	biennial Lettuce
LAROCC	Larix occidentalis	Western Larch
LATOCH	*Lathyrus ochroleucus	Cream-flowered Peavine
LIGCAN	*Ligusticum canbyi	Canby's Licorice-root
LINBOR	Linnaea borealis	Western Twinflower
LONINV	*Lonicera involucrata	Bearberry Honeysuckle
LONUTA	Lonicera utahensis	Utah Honeysuckle
LUZPAR	*Luzula parviflora	Small-flowered Woodrush
LYSCIL	*Lysimachia ciliata	Fringed Loosestrife
MELSMI	*Melica smithii	Smith's Melic
MELSUB	*Melica subulata	Alaska Oniongrass
MENARV	*Mentha arvensis	Field Mint
MENFER	*Menziesia ferruginea	Fool's Huckleberry
MERPAN	*Mertensia paniculata	Panicle Bluebells

* - voucher specimen collected
? - most probable identification based on reference material collected

Table A. Continued.

Alpha	Scientific Name	Common Name
MITBRE	*Mitella breweri	Brewer's Mitrewort
MITNUD	*Mitella nuda	Bare-stemed Mitrewort
MITPEN	*Mitella pentandra	Five-stamened Mitrewort
MITTRI	*Mitella trifida	Three-tooth Mitrewort
MONCOR	*Montia cordifolia	Broad-leaf Montia
MONSIB	*Montia siberica	Western Springbeauty
OPLHOR	*Oplopanax horridum	Devil's Club
OSMCHI	*Osmorhiza chilensis	Mountain Sweet-root
OSMOCC	*Osmorhiza occidentalis	Sweet Anise
PACMYR	*Pachistima myrsinites	Myrtle Boxwood
PARFIM	*Parnassia fimbriata	Fringed Grass-of-parnassus
PEDBRA	*Pedicularis bracteosa	Bracted Lousewort
PETSAG	*Petasites sagittatus	Arrowleaf Coltsfoot
PHAARU	*Phalaris arundinacea	Reed Canarygrass
PHLPRA	*Phleum pratense	Common Timothy
PICENG	Picea engelmannii	Engelman Spruce
PINCON	Pinus contorta	Lodgepole Pine
PINMON	Pinus monticola	Western White Pine
PINPON	Pinus ponderosa	Ponderosa Pine
PLAMAJ	*Plantago major	Common Plantain
PLAMPI	*Plantago major var. pilgeri	Pilger's Plantain
POAPAL	*Poa palustris	Fowl Bluegrass
POAPRA	*Poa pratensis	Kentucky Bluegrass
POLOCC	*Polemonium occidentale	Western Polemonium
POLPUL	*Polemonium pulcherrimum	Skunk-leaved Polemonium
POLDOU	*Polygonum douglasii	Douglas' Knotweed
POLLON	*Polystichum lonchitis	Mountain Hollyfern
POPTRE	Populus tremuloides	Quaking Aspen
POPTRI	*Populus trichocarpa	Black Cottonwood
POTGRA	Potentilla gracilis	Northwest Cinquefoil
POTNOR	*Potentilla norvegica	Norwegian Cinquefoil
PRUVUL	*Prunella vulgaris	Self-heal
PRUVIR	Prunus virginiana	Common Chokecherry
PSEMEN	Pseudotsuga menziesii	Douglas Fir
PTEAQU	*Pteridium aquilinum	Brakenfern
PTEAND	*Pterospora andromedea	Woodland Pinedrops
PYRASA	*Pyrola asarifolia	Pink Wintergreen
PYRCHL	*Pyrola chlorantha	Green Wintergreen
PYRELL	*Pyrola elliptica	White Wintergreen
PYRMIN	*Pyrola minor	Snowline Pyrola
PYRSEC	*Pyrola secunda	One-sided Wintergreen
PYRUNI	*Pyrola uniflora	Woodnymph

* = voucher specimen collected
? = most probable identification based on reference material collected

Table A. Continued.

Alpha	Scientific Name	Common Name
RANABO	*Ranunculus abortivus	Small Flowered Buttercup
RANUNI	*Ranunculus uncinatus	Little Buttercup
RHAALN	*Rhamnus alnifolia	Alder Buckthorn
RHAPUR	*Rhamnus purshiana	Cascara
RIBHUD	*Ribes hudsonianum	Hudson Bay Currant
RIBINE	*Ribes inerme	Whitestem Gooseberry
RIBLAC	Ribes lacustre	Swamp Current
RIBOXY	*Ribes oxyacanthoides	Northern Gooseberry
ROSACI	*Rosa acicularis	Prickly Rose
ROSGYM	Rosa gymnocarpa	Baldhip Rose
RUBIDA	*Rubus idaeus	Red Raspberry
RUBPAR	Rubus parviflorus	Thimbleberry
RUDOCC	Rudbeckia occidentalis	Blackhead Coneflower
RUMOBT	*Rumex obtusifolius	Bitter Dock
SALBAR	*Salix barclayi	Barclay's Willow
SALDRU	*Salix drummondii	Drummond Willow
SALEXI	*Salix exigua	Sandbar Willow
SALSCO	Salix scouleriana	Scouler Willow
SAMRAC	Sambucus racemosa	Red Elderberry
SANMAR	*Sanicula marilandica	Black Snake-root
SAUAME	*Saussurea americana	American Saw-wort
SENFOE	*Senecio foetidus var. hydrophiloides	Sweet-marsh Butterweed
SENPSE	*Senecio pseudaureus	Golden Groundsel
SENTRI	*Senecio triangularis	Arrowleaf Groundsel
SHECAN	Shepherdia canadensis	Canada Buffaloberry
SMIRAC	Smilacina racemosa	False Spikenard
SMISTE	Smilacina stellata	Starry Solomon-plume
SOLCAN	*Solidago canadensis	Canada Goldenrod
SORSCO	*Sorbus scopulina	Cascade Mountain-ash
SPIBET	Spiraea betulifolia	Shiny-leaf Spirea
SPIDEN	*Spiraea densiflora	Subalpine spirea
SPIDOU	Spiraea douglasii	Douglas Spirea
STECAL	*Stellaria calycantha	Northern Starwort
STECRI	*Stellaria crispa	Crisped Starwort
STELOG	*Stellaria longifolia	Longleaved Starwort
STRAMP	Streptopus amplexifolius	Clasping-leaved Twisted-Stalk
SYMALB	Symphoricarpos albus	Common Snowberry
TAROFF	Taraxacum officinale (?)	Common Dandelion
TAXBRE	*Taxus brevifolia	Mountain Yew
TELGRA	*Tellima grandiflora	Fingecup
THAOCC	Thalictrum occidentale	Western Meadowrue
THUPLI	Thuja plicata	Western Redcedar

* - voucher specimen collected
? - most probable identification based on reference material collected

Table A. Continued.

Alpha	Scientific Name	Common Name
TIAUNI	*Tiarella trifoliata var. unifoliata	Coolwort Foamflower
TRADUB	Tragopogon dubius	Yellow Salsify
TRIPRA	*Trifolium pratense	Red Clover
TRIREP	*Trifolium repens	White Clover
TRIOVA	Trillium ovatum	White Wake-robin
TRICAN	*Trisetum canescens	Tall Trisetum
TRICER	*Trisetum cernuum	Nodding Trisetum
TSUHET	Tsuga heterophylla	Western Hemlock
URTDIO	*Urtica dioica	Stinging Nettle
VACGLO	Vaccinium globulare	Globe Huckleberry
VACMYR	Vaccinium myrtillus	Dwarf Bilberry
VACSCO	Vaccinium scoparium	Grouse Whortleberry
VERVIR	Veratrum viride	Green False Hellebore
VERTHA	Verbascum thapsus	Flannel Mullein
VERAME	*Veronica americana	American Speedwell
VERSER	*Veronica serpyllifolia	Thymeleaf Speedwell
VICAME	*Vicia americana	American Vetch
VIOCAN	*Viola canadensis	Canada Violet
VIOGLA	*Viola glabella	Pioneer Violet
VIOORB	Viola orbiculata	Round-leaved Violet
XERTEN	Xerophyllum tenax	Beargrass
ZIGELE	*Zigadenus elegans	Glaucous Zigadenus

* - voucher specimen collected
? - most probable identification based on reference material collected